TEXT-BOOK OF BOTANY

(INDIAN EDITION)

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LOWSON'S

TEXT-BOOK OF BOTANY

(*INDIAN EDITION*)

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WITH A PREFACE BY

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PREFACE.

THE number of students in India who take up Botany for elementary examinations is surprisingly large when one recognises the fact that until quite recently there have been no good elementary treatises in which Indian types of vegetation were dealt with. Though allowance must be made for the extraordinary capacity which oriental students show for committing to memory, with a remarkable comprehension, bookwork upon every conceivable subject, this would seem to indicate that there exists among the natives of India a real interest in plants. It is to meet this halfway, and to encourage this desire to know about plants, their structures and functions, that the present adaptation of Mr Lowson's well-known manual is published.

Mrs Willis was very successful in the teaching of botany at a high grade school in Ceylon, where for some years she gave voluntary lessons, and she may consequently lay claim to some local experience Her teaching followed "Nature-study" lines, and it was found that the girls took a keen interest in the actual plants, their parts, the functions of those parts, and in simple experiments to prove the nature of those functions. All these questions are well treated by Mr. Lowson, and in particular he gives many experiments upon functions, which will be found of very great interest when by the substitution of Indian for European plants they are made more easily available to students living in

eastern countries In general only those plants are given that Mrs Willis has herself found suitable for the demonstration of these or similar experiments.

The great failing of the eastern student is his tendency to learn by rote He is better at abstract studies than at concrete, but that he has some liking for the latter is shown by the frequency with which he takes up the study of botany and kindred sciences. This tendency to prefer abstract studies is one which should as far as possible be checked and controlled by the simultaneous study of concrete, of which one of the very best for most people is botany, since for this subject the necessary material is available by every roadside and, in India, at any time of year with a book adapted to Indian requirements he should obviously feel more at home than with one which deals with the wallflower and the bluebell, and other types unfamiliar in India

One great difficulty that has come up in the choice of the types for study in India is that the country is so enormous, and includes such a variety of climates, from cold to hot, from wet to dry, that the flora is by no means so uniform all over it as it is for example in the British Islands Madras and the Punjab, for instance, have comparatively few plants in common. It is hoped that the particular examples chosen may prove to be sufficiently common to be within the reach of everyone, and in this connection it is a pleasure to acknowledge the assistance given by Mr. I. H Burkill, M.A , Director of the Botanic Gardens of Singapore, and lately Reporter on Economic Products to the Government of India.

The student who has mastered this book, and successfully performed the experiments described therein, must not think that he has yet acquired a good knowledge of Botany, but only of the methods employed in obtaining

that knowledge. He will be familiar with the lines upon which to work in obtaining that further acquaintance which will ultimately entitle him to claim a good understanding of the subject This caution is by no means unnecessary, as a very limited amount of study is often considered by its owner as entitling him to pose as thoroughly acquainted with the subject Having mastered this book the student should be better able to follow up the subject, and may even be ready to take up work upon his own account

There are many floras of different parts of India now published or in course of publication, and a very brief study of one of these will show how much there is to be done before our knowledge of the local distribution of the plants of India can approach completeness If a student will work with one of these floras for the district in which he resides, making collections of the local plants, identifying them with the flora, and preparing an herbarium with the localities carefully marked, the flowering seasons given, and all other possible notes made about the plants, he may render very useful service to the study of the flora of India, and when he becomes a master of his subject may begin to publish papers upon the local flora.

Still more useful, perhaps, will be he who studies the ecology of the local flora—the problem of the life of plants in relation to their natural environment—going carefully into the whole subject, with the necessary experiments for clearing up various problems Here, again, some years must be spent in work, which will, however, be found both interesting and attractive, before the student can hope to be in a position to publish his results.

Both these lines of work are open to the trained amateur, and in a few years he may hope to reach the stage of publishing his observations, whereas in such subjects as

physiology or anatomy very special training is required, and the amateur cannot easily do good work But whether he carry on work to the stage of publication or not, the amateur will find the study of the botany of his neighbourhood a very fascinating one, and he will get variety when he visits the hills or the coast.

RIO DE JANEIRO, J. C. WILLIS
July, 1913

NOTE ON SECOND EDITION.

IN this revision of the first Indian edition of this book, which was an adaptation by Mrs J C Willis of Mr Lowson's well known *Text-book of Botany*, the chief aims have been first to introduce new matter into the chapters on the Natural Orders dealing specifically with the Indian Flora, and next to introduce as many more as possible of the better known vernacular plant names

The Natural Orders have been placed in two consecutive chapters, and their sequence has been altered to conform more closely to that of Engler's system. Several Natural Orders have been added, and it has been found possible to introduce a considerable number of vernacular names, of which the book now contains about two hundred and fifty, including many familiar household words

If a student wishes to find the Latin or English equivalent of a vernacular name, he should consult the Vernacular

Index at the end of the book. If he wishes to find the vernacular equivalent of an English or Latin name, he should consult the General Index

The chief difficulty in preparing a book on Botany for Indian use is naturally the diverse nature of the flora in different regions of India. The flora of India strikes the English student as being predominantly tropical, and this impression is entirely justified. Yet it is too often ignored that the character of the North-west Himalayan flora, especially between the heights of 5,000 and 11,000 feet, is strikingly European. A native of England who visits Kashmir, Simla or other hill stations on the Panjab cannot fail to notice numerous plants with which he is already acquainted. To mention only a few instances, he would meet with the Chickweed (*Stellaria*), Crowfoot and Buttercups (*Ranunculus*), the Marsh Marigold (*Caltha Palustris*), species of *Clematis*, Columbine (*Aquilegia*), Monkshood (*Aconitum*), numerous species of *Rubus* (Bramble, Raspberry, Blackberry, etc.), Dead Nettle (*Lamium*) and Wild Mint In the upper reaches of the Himalayas, too, the Alpinist would find the well known Edelweiss (*Leontopodium alpinum*), as well as species of *Potentilla* and other genera which in Europe grow at a much lower level

In the case of these and other popular English names occurring frequently in the course of the book it is futile, at present, to attempt to give the vernacular equivalents. In all cases of economically unimportant plants these names have only a local application, and are moreover very difficult to ascertain accurately.

In addition to the changes mentioned above, the book has been thoroughly revised, and certain portions have been rewritten and enlarged, especially Chapter XV.

Several friends from different parts of India have given me valuable help and made useful suggestions with regard to the work. To these I have pleasure in offering my hearty thanks.

BIRBAL SAHNI

CAMBRIDGE, 1919

NOTE ON THIRD EDITION.

THE chief alteration in this Edition is the insertion of a new and important chapter on Evolution and Genetics.

October, 1922

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PART III.—VASCULAR CRYPTOGAMS AND FLOWERING PLANTS.

PART IV.—THE LOWER CRYPTOGAMS.

TEXT-BOOK OF BOTANY.

INTRODUCTORY.

§ 1 **Botany** is the science which deals with the phenomena of plant-life. It considers the form and structure of plants, their functions and life-histories; it studies the various processes of their growth and development; and, by carefully noting the resemblances and differences discernible between them, it attempts to draw up a scheme of classification, expressing as clearly as possible their affinities or relationship to one another.

§ 2. **Subdivisions of the Science.**—Plants, like animals, may be studied in different ways or from different points of view These constitute different subdivisions or departments of Botanical Science, of which the most important are **Morphology** and **Physiology**. We may indicate the scope of these by considering a particular plant—let us say the Sunflower.

Naturally we should first of all give our attention to external features. We should find that the plant consists of certain well-defined parts or **members**—roots, stems, leaves, flowers, etc.; that, speaking generally, these have approximately the same forms in all sunflowers of the same species, while they differ in many respects from those of other plants; that the stem branches, and the branches have a definite position in relation to the leaves

By comparing the relative positions of the members in the Sunflower with those in other plants it would be possible to draw up a classification of plant-members. A study of this kind, dealing with the external forms and relative positions of plant-members, is called **External Morphology.**

We might then wish to get some knowledge of the internal parts of these various members. For this purpose we should take sections of the stem, root, leaf, etc, or examine these in various other ways. Such a study, dealing with internal structure, is called **Internal Morphology.** It may be carried on in two ways. First, we might content ourselves with the naked-eye appearance of the internal parts, and examine only the coarser features This is **Anatomy.** Secondly, we might undertake a closer study with the help of the microscope, and make out the finer features of structure—the cells and tissues of the plant-body. This is **Histology.** *Cytology*, the study of cell-structure, is a branch of Histology which has been greatly developed in recent years.

Evidently, then, *Morphology* has regard only to the form and structure of plants, and pays no attention to the vital processes which are carried on But we might carry our morphological studies much further than this Instead of examining the Sunflower at any one particular stage in its growth, we might study the form and structure exhibited through all the stages, and observe the changes which take place

Beginning with the seed, we could make out the parts of the embryo plant contained in the seed, we could notice the gradual growth of the root and stem, and the formation of leaves; we could study the origin and growth of branches; finally, we could make a study of the flower and investigate the morphological changes which lead up to the formation of another seed This is a study of **Development.** It seeks to discover the earliest beginnings of the organism and to trace the changes and modifications which occur in passing from one stage to another. Development might be defined as a history of the morphology of an organism As distinguished from

individual development, which is called *Ontogeny*, the development of the race or species to which the plant belongs, *i e.* its genealogy, or evolutionary history, is spoken of as its *Phylogeny*.

Another morphological study is **Classification.** It is based on Comparative Morphology and Development. Here the forms and structures of plants in all stages of their life-histories are studied and compared, and according to the resemblances and differences perceived the plants are arranged or classified.

The physiologist, pure and simple, would approach our Sunflower plant in quite a different frame of mind. Neglecting for the moment its form and structure, he would set himself such questions as :—How does the plant obtain nourishment? What is the nature of its food-material? How are these food-materials assimilated? What is growth? What processes are carried on in connection with growth? How is the plant affected by its environment? What influence have light, heat, etc., on plant growth? How is reproduction carried on?—etc. To give an answer to these and all such questions belongs to **Physiology.** Thus Physiology concerns itself with the various life-processes—that is, with the functions necessary for the welfare of the individual and the perpetuation of the species. In this connection the various parts of the organism are considered as **organs** adapted to the performance of various functions.

Morphology and Physiology ought not to be regarded as separate and independent studies Harmonious cooperation results in mutual benefit. The study of form and structure is barren and unprofitable apart from the study of function, and, on the other hand, the study of function demands, as a necessary condition, a minute and careful study of form and structure. The recognition of this in recent years has led to the rapid development of one of the most important and interesting departments of Botanical Science, namely, the study of how the form and structure of plants are adapted to the conditions of their environment. This study, which is both morphological and physiological, is known as **Ecology** (or *Oecology*).

§ 3. **General Classification of the Plant Kingdom.**—There is no need to enlarge on the infinite variety of form presented in the Vegetable Kingdom. The beginner in Botany is sufficiently impressed with it. The refuge from hopeless confusion is found in Classification. At the outset a certain advantage will be obtained if the student obtains a bird's-eye view, as it were, of the country he is about to enter. For this reason, and also because it will serve as a convenient table of reference, we venture at this early stage to give a *general* classification indicating clearly the position of the various plant-types we shall consider in the following pages.

In very much the same way as we might ask the student to think of a bird, a fish, an insect, and a mussel, and notice how very different they are from each other, so we would ask him to consider and contrast four plant-types—namely, a buttercup, a fern, a moss, and a seaweed. In a general way, he will recognise that they present considerable differences from each other: the Buttercup alone has flowers; the Fern has a stout underground stem, roots and leaves; the Moss is a much more delicate plant, with stem and leaves but no true roots; the Seaweed bears no members resembling the stem and leaves of the other types. Now these four plants may be taken as types of the four chief groups of the Plant Kingdom. These and the more important subdivisions are represented in the following scheme:—

A. **Thallophyta.**

(i) **Schizomycetes,** commonly known as Bacteria.

(ii) **Algæ**—mostly aquatic plants, including the Seaweeds and various fresh-water forms, e.g. *Pleurococcus, Chlamydomonas, Sphærella, Spirogyra, Vaucheria, Oedogonium, Fucus.*

(iii) **Fungi,** including Moulds, Toadstools, etc.; e.g. *Mucor, Pythium, Eurotium, Saccharomyces, Agaricus.*

B **Muscineæ** or **Bryophyta,** including the Liverworts and Mosses, e g. *Pellia, Funaria.*

C. **Pteridophyta,** or **Vascular Cryptogams,** *e.g.* Ferns, Horsetails (*Equisetum*), Selaginellas, and Club-mosses (*Lycopodium*).

D. **Phanerogams, Spermaphyta or Flowering Plants.**

(i) **Gymnosperms,** e.g. *Pinus*, the Pine, the commonest species of which is *Pinus sylvestris,* known as the Scots *Fir*; also Larch, Spruce, Yew, Juniper, Cedar, Cypress, etc.

(ii) **Angiosperms**—the highest or typical Flowering Plants.

(*a*) **Monocotyledons,** *e g* Grass, Lily, Narcissus, Orchid, etc

(*b*) **Dicotyledons,** *e g.* Sunflower, Buttercup, Rose, etc.

The Flowering Plants were called **Phanerogams** because, bearing flowers and forming seed, their method of reproduction was regarded as clear or evident (Gr. φανερος, *evident*; γαμος, *marriage*); the other groups, Thallophyta, Bryophyta, and Pteridophyta, were grouped together as **Cryptogams,** because their reproductive processes, it was thought, were hidden or concealed (Gr. κρυπτος, *hidden*; γαμος). These terms are still retained, although they have lost their original significance The reproduction of the Cryptogams has been fully elucidated, and, as a matter of fact, is more evident than that of the Phanerogams.

PART I.—GENERAL.

CHAPTER I.

EXTERNAL MORPHOLOGY AND PHYSIOLOGY.

§ 1. **Unicellular and Multicellular Plants.**—The lowest plants are of microscopic size and have a very simple structure. In the simplest forms of Algæ, for example, each individual (Fig 1) consists of a little round sac or vesicle filled with a slimy granular substance called *protoplasm*, in which is embedded a denser protoplasmic body, the nucleus, along with others, one or several, called chloroplasts, through the substance of which is diffused a green colouring matter called chlorophyll. Such a structure is called a cell. The lowest forms of plant-life are one-celled or unicellular. In all the higher forms the plant-body is multicellular, *i.e.* it consists of numbers of cells aggregated together and closely united with each other.

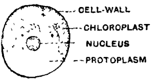


Fig 1.—A Unicellular Alga

§ 2 **Differentiation.**—In unicellular plants all the vital functions are carried on by the single cell, but in multicellular forms, as a rule, different parts of the organism take on different functions, and each part has a form and structure adapted to the performance of its particular function. Members which have special forms adapting them to the performance of particular functions are said to be *specialised*. Thus the organism consists of parts or

members differing from each other. Seeing that these various functions are carried on for the good of the organism as a whole, it is evident that in such an organism there is **Division of Labour.** The distribution of functions which characterises this division of labour is called **Physiological Differentiation**; and the marking off of distinct members serving as the organs of particular functions, which is correlated with it, constitutes **Morphological Differentiation.**

It is evident that morphological and physiological differentiation go hand in hand. In the lower forms, the functions carried on are very simple and general, and there is comparatively little division of labour, so that morphological differentiation is only slightly marked. As we ascend from lower to higher forms, however, we find that the arrangements become more and more numerous and complex, and the division of labour correspondingly extensive. Hence it is in the highest plants that we meet with the most pronounced and far-reaching differentiation of members As a matter of fact, speaking generally, we distinguish between lower and higher forms by the degree of differentiation and division of labour exhibited in each case

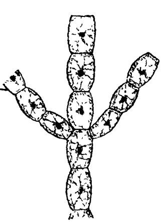


FIG. 2.—PART OF A BRANCHED FILAMENTOUS THALLUS.

§ 3. The Thallus.—Amongst the Thallophyta (p. 4) the plant-body is very simple. It may be unicellular; when multicellular, it usually consists of a flattened membranous expansion, or of a mass of branched or unbranched filaments (Fig. 2) Various members are in many cases more or less distinctly differentiated. As a rule, however, there is no clearly

marked separation into distinct members corresponding to the root, stem, and leaf of higher plants. In the higher forms only of Thallophyta do we find indications of such a differentiation. For the most part, the lateral outgrowths reproduce the structure of the part from which they spring. A vegetative structure of this kind is called a **thallus.** It is specially characteristic of the Algæ and Fungi, although not confined to these; hence the name Thallophyta for the division in which they are placed

§ 4. **Shoot and Root.**—In plants above the Thallophytes, the plant-body usually exhibits a differentiation into distinct members, which becomes more marked and more complex as we pass from lower to higher types In these plants a descending portion, which serves to fix the plant in the soil and absorb nourishment, is usually clearly distinguished from a part whose tendency is to pass upwards towards the light These parts are known as the *root* and the *shoot.* In the Bryophyta, however, a true root is never differentiated, and in many Liverworts the vegetative structure is a thallus The shoot is nearly always further differentiated into **stem and leaf** (leafy shoot). The differentiation of root and shoot probably arose in adaptation to terrestrial conditions of life—the earlier and more primitive plants being aquatic Thallophytes.

§ 5 **Vegetative Shoot and Reproductive Shoot.**—In many Vascular Cryptogams the same shoot carries on the nutritive or *vegetative* functions and bears the reproductive organs; but in others there is a differentiation of two kinds of shoots—one purely vegetative, the other reproductive This differentiation is carried still further in the Flowering Plants, where the reproductive shoots (floral region of the plant) are clearly marked off in most cases from the vegetative shoots (the foliage region). Our conceptions of stem and leaf structures are derived from a consideration of the foliage or vegetative region of the plant. Nevertheless, the *flower*, although in appearance altogether different, consists, like the foliage or vegetative shoot, of stem and leaf structures The differences are due

to the fact that in the floral region these structures have entirely different functions to discharge.

§ 6 **Higher Differentiation or Specialisation of Members.**—In the Flowering Plants, the members take on very various and often highly specialised or complex functions. In each case the special form and structure of the member are adapted to the performance of its special function. This is why in the Flowering Plants we meet with such a manifold diversity of form. When the specialisation is of a very extreme character, there is often a difficulty in recognising the morphological value of the structures under consideration — as *e.g.* in the Pitcher Plant, where the leaves take the form of pitchers.

In the vegetative region of plants, stems, leaves, and roots have undergone many interesting modifications with which we shall have to deal in detail when we come to consider fully the morphology of these members. At present it is desirable that the student should recognise that these modifications have arisen simply as adaptations to a special environment and for the performance of special functions.

§ 7. **Plant-Members.**—Thus in the higher plants three chief categories of members—members of the first rank—are recognised, viz: **roots, stems,** and **leaves.** According to the various well-marked specialisations met with, these may be subdivided into members of secondary rank, thus leaves may be subdivided into foliage leaves, floral leaves, and so on. And these again may be subdivided. In each category or group the members are **morphologically similar**, but members belonging to different groups are **dissimilar**. Thus stem and leaf, stem and root, are examples of dissimilar members.

§ 8. **Appendages or Outgrowths.**—In addition to members which are included in one or other of the above categories, other members of subordinate rank are found in plants. They are of the nature of appendages or outgrowths of the members of the first order. Their forms

are innumerable, for they include all the different kinds of hairs, prickles, etc. They may be developed on all parts of the plant, but chiefly on stem and leaf structures.

§ 9. **Symmetry of Plant-Members.**—Plant-members usually exhibit more or less well-marked symmetry. They may be divided in certain directions so as to give similar halves. The forms and degrees of symmetry are various, the two chief ones being:—

(a) **Radial Symmetry.**—Where the member can be divided into similar halves by a number of planes (two or more) passing through some particular axis

(b) **Bilateral Symmetry.**—Where the member can be so divided by only one or, at most, two planes.

For example, most stems and roots have radial symmetry; they are *usually* perfectly symmetrical round their longitudinal axis; so also many flowers, and a few cylindrical leaves (*centric* leaves, *e g.* the Onion).

There are two kinds of **bilateral symmetry**:—

(i) The member may be divisible in two planes at right angles In this case the halves formed by division along one plane resemble each other, but differ from the halves formed by division along the other plane. Thus the walnut may be divided along the line which separates the two valves of the fruit, or at right angles to this. So also the leaf of the Iris. It is a vertical leaf and shows similar right and left surfaces. It may be divided longitudinally either parallel to these surfaces or at right angles to them This form of symmetry is known as the **isobilateral**.

(ii) There may be only one plane of symmetry. Here the symmetry is **zygomorphic** and the member is monosymmetrical. Examples of this are common. It is seen in many flowers, *e g* the Pea or Violet. When the zygomorphic symmetry is such that distinct lower and upper surfaces can be distinguished, the members are said to be

dorsiventral. This is the case in the common or *bifacial* type of leaf. Sometimes, however, bifacial leaves, owing to greater development on one side, are asymmetrical, *i.e.* have no plane of symmetry at all, *e.g.* the leaf of the Lime.

§ 10. **Branching of Members.**—The various members of a plant may bear other members either like or unlike themselves, *i.e.* similar or dissimilar. Thus roots may bear lateral secondary roots, *i.e* similar members; stems may bear secondary stems and leaves, *i.e.* both similar and dissimilar members The development of similar members is called *branching*.

There are two chief ways in which branches may be produced —two chief types of branching.—(*A*) **dichotomous branching** (Fig. 3, A); (*B*) **lateral branching** (Fig 3, B, C).

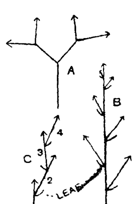


Fig 3.—FORMS OF BRANCHING A, Dichotomous, B, Racemose, C, Cymose.

In dichotomous branching the growing apex of a stem or a root is divided into two and each part grows out into a branch. The branching in this case consists of a series of bifurcations. True dichotomy is comparatively rare, at least in the higher plants. It probably does not occur at all in the Flowering Plants; but examples of dichotomous branching are found in the Vascular Cryptogams and Bryophyta, and are common amongst Thallophytes.

In lateral branching the branches arise as lateral outgrowths a short distance behind the extreme apex of the growing region of the parent member. This is the characteristic mode of branching in the Flowering Plants.

If the parent member continues to grow, and develops numerous lateral branches, one after the other, the lateral branching is said to be **indefinite** or **racemose** (Fig. 3, B).

If, as is nearly always the case, these numerous lateral branches are produced in regular order, and in such a way that the youngest lie nearest the apex, they are said to be developed in *acropetal succession*.

If, however, the parent member ceases to grow after producing one or a very few branches, and the growth is continued by these branches repeating the process, the lateral branching is said to be **definite** or **cymose**. Thus in Fig. 3, c, axis 1 produces axis 2 and ceases to grow; 2 produces 3; 3 produces 4; and so on.

A. *Dichotomous*.

B. *Lateral*.

(*a*) *Indefinite* or *Racemose* (Monopodial).

(*b*) *Definite* or *Cymose*

Here we have a general table of branching which will be supplemented and illustrated in connection with the detailed description of the morphology of roots, stems, leaves, and inflorescences

§ 11. **Nutrition and Growth.**—We have already seen that the lowest forms of plants are unicellular. In typical cases the cell (§ 1) consists of a nucleated speck of protoplasm containing one or more chloroplasts and enclosed in a delicate membrane or cell-wall. The protoplasm is the *living* substance of the cell The cell-wall merely supports and protects the protoplasm. If we examine such an organism carefully we find that it grows in size and reproduces itself Now it is evident that there must be some source from which it draws food-materials, and certain vital processes or functions must be carried on in order that these materials may be assimilated or built up into its own substance These processes are the same in kind as are carried on by all green plants, but in these unicellular plants they are all performed by a single cell, and may therefore be studied in their simplest forms.

The first consideration is that food-materials, of whatever kind they may be, cannot, owing to the presence of a definite cell-wall, enter the cell in solid form, but must do so in solution. Here we have what is sometimes

regarded as a fundamental distinction between a plant and an animal. All plants take in their food-material in solution.

Our green unicellular plant grows either in water or on some moist substratum. The water, with various substances in solution, passes by diffusion through the cell-wall and is absorbed into the interior of the cell. The dissolved substances are of a very simple character. The most important of them are certain mineral substances, such as nitrates, sulphates, phosphates, and carbon dioxide (CO_2). Here we have another important point of distinction between an ordinary green plant and an animal. Green plants take in their food-material in the form of simple *inorganic* substances. Animals cannot live on simple inorganic substances, they must feed on complex *organic* compounds, such as carbohydrates, fats and oils, and proteids.

The question now arises—how are these simple compounds built up into living protoplasm, which is an extremely complex unstable substance containing carbon, oxygen, hydrogen, nitrogen, sulphur, and phosphorus, but whose exact composition has not yet been determined? The building up of a complex unstable substance from simple stable substances necessitates the expenditure of a certain amount of energy. In animal nutrition this energy is derived from the food-materials themselves. The proteids, fats, and carbohydrates absorbed contain a large store of potential energy. Little or no energy can, however, be obtained from the very simple inorganic substances assimilated by green plants. What, then, is the source of energy? The answer will be clear if we consider the conditions of assimilation.

It has been determined that from the water and carbon dioxide absorbed certain organic compounds of the nature of carbohydrates are formed. This process is called **carbon assimilation** or **photosynthesis**. It requires the presence of light and of chlorophyll. The conclusion we come to is that sunlight is the source of energy, and that chlorophyll is a substance which enables the plant to make use of this radiant energy, just as the manufacture of cloth

from raw fibre requires not only some form of energy, but also a special mechanical apparatus. More complex compounds are then elaborated, containing nitrogen derived from the absorbed nitrates. Finally these complex compounds are made use of by the protoplasm in building up its substance.

If the student carefully reflects on the process so far described he will recognise that in both plants and animals living protoplasm makes use of complex compounds in building up its substance, but, whereas animals derive these compounds already manufactured (by feeding on plants or other animals), the green plant must elaborate them for itself from the simple inorganic solutions which it absorbs. Hence the necessity (in most plants—see § 12) for the presence of chlorophyll and for exposure to light. The plant, as it were, starts its chemical processes at a lower level than the animal.

Thus the protoplasm in our unicellular plant obtains nourishment and increases in amount. But what of the cell-wall? It also must increase in surface-extent. How is this effected? The cell-wall consists chiefly of a substance called cellulose, much simpler in composition than protoplasm. During growth new molecules of cellulose are formed from the protoplasm and are deposited in the cell-wall. Now a complex substance to produce a simpler substance must undergo decomposition The growth of the cell-wall, then, implies decomposition of protoplasmic substance.

This is characteristic of all growth. Not only are there synthetic or "building up" processes which may result in the elaboration of protoplasm, but there are also "breaking down" processes, processes of decomposition. The former are called **anabolic**, and constitute **anabolism**; the latter **katabolic**, and constitute **katabolism**. The sum-total of the chemical processes going on, anabolic and katabolic, constitutes **metabolism**.

This decomposition of the protoplasm is a process of oxidation; in connection with it there is an absorption of oxygen; in other words, there is a process of **respiration** similar to what goes on in animals. The decomposition

results in the formation of certain substances, of which some are directly used in building up the substance of the plant (*plastic substances*), others are only indirectly useful (*secretions*), and others finally have no evident use (*excretions*). The decomposition also sets free a certain amount of energy. In plants this is chiefly expended in the processes of growth, although a certain amount may be dissipated in other ways

Here again we may institute a comparison between plants and animals. In animals [redacted] katabolic processes are active In a full-grown animal the loss of matter (by excretion) and of energy in katabolism nearly equals the gain made in anabolism. This is correlated with the much greater activity exhibited by the animal organism. In plants, on the other hand, anabolism is greatly in excess of katabolism, so that in plants there is continual increase in the amount of plant-substance. This is correlated with the passivity and lack of movement characteristic of plants. The animal is essentially active and katabolic, while the plant is essentially passive and anabolic.

Although we have described the general processes of metabolism with special reference to a unicellular plant, they hold good for all green plants Thus a seaweed absorbs simple inorganic solutions over its whole surface. These pass from cell to cell through the whole plant, and are elaborated as above described.

In higher plants, special members are developed to perform the work of absorption. The root serves to fix the plant and absorbs solutions of mineral salts from the soil. In root, stem, and leaf a system of conducting tissue is developed, by means of which the solutions absorbed by the root are conveyed to the leaves. The foliage leaf is the *chief* organ for the absorption of carbon dioxide which is derived from the atmosphere. In the cells of the leaf elaboration of these food-materials is carried on. The complex organic compounds thus formed are distributed over the plant and are made use of by the living protoplasm. In addition to this the leaves are active respiring organs and also give off large quantities of water-vapour (process of **transpiration**).

§ 12. **Plants without Chorophyll.**—Some plants have no chlorophyll, *e.g.* the Fungi and a few flowering plants From what has been said above it will be evident that these plants cannot assimilate simple inorganic food-materials. They can only make use of food-material consisting of complex organic compounds. In this respect they resemble animals, but the compounds are simpler than those required by animals These complex compounds may be obtained either from living organisms or from decaying organic substance. In the former case the plants are **parasites.** They send down absorbing organs into the tissues of some living plant or animal (called the *host*), and thus obtain their nutritive material. In the latter case they are called **saprophytes.**

§ 13. **Reproduction.**—Two methods of reproduction are met with in plants:—(*a*) **asexual** or **agamogenetic**; (*b*) **sexual** or **gamogenetic.** The asexual method consists essentially in the separation from the parent organism of a part which grows directly into a new organism. The part separated off may be simply a more or less specialised portion of the vegetative region, *e g* the potato-tuber. This is *vegetative reproduction* If it is a highly specialised single reproductive cell (**spore**) it is *asexual spore-reproduction.* In vegetative reproduction the new organism produced resembles the parent, in asexual spore-reproduction this may or may not be the case.

The sexual method consists in the separation of two sexual cells (**gametes**), each of which is incapable *by itself* of producing a new organism, but which fuse together and produce a new cell (**the zygote,** or sexually produced spore) with altogether new properties, which is able to develop into a new plant In many Thallophyta the gametes are similar. In the higher types they are clearly differentiated into male and female—the former (*e.g.* spermatozoid) corresponding to the spermatozoon of the animal, the latter to the ovum.

A *spore* may be defined as a highly specialised reproductive cell which is capable by itself of giving rise to a new organism. It may be produced sexually or asexually.

§ 14 **Relation to Environment.**—The intimate relation which exists between a plant and its environment is shown by the fact that plant-members always have a form and structure adapted to the particular conditions in which the plant lives. These forms and structures can only be explained by a reference to these conditions. A plant which is not adapted to or in harmony with its surroundings dies. The living protoplasm is constantly subjected to the stimulating influence of external agencies, such as light, heat, gravity, etc, and it is constantly responding in particular ways to these influences. We shall have to consider some of the results of this on growth in a later chapter (VIII.).

§ 15. **Homology and Analogy.**—In the course of this chapter we have suggested two distinct principles of the highest importance to the biological student. We may now clearly explain and state them. We have seen that a study of morphology leads to the recognition of similar members, *i e* morphologically similar. Thus stems, whatever their special form, are similar members. So also leaves. Members morphologically similar are said to be homologous, or the *homologues* of each other. Homologous members or structures are recognised by the relations of their position and development. **Homology** is the term by which we express a resemblance existing between various members as regards their position and development. We have seen, however, that homologous members may take on many different forms according to the functions which they carry on. Thus foliage leaves, floral leaves (sepals, petals, etc., of a flower), although homologous, have distinctly different forms.

On the other hand, in some plants the climbing organs called tendrils are morphologically leaves or leaflets, *e.g.* in the Pea; while in others, *e.g.* in the Vine, they are morphologically stems. Here we have structures apparently similar, namely tendrils. Yet they are not homologous. Their resemblance to each other is physiological, not morphological. They have similar functions, and have therefore, by way of adaptation, assumed the same form.

Members which present resemblances of this kind are said to be analogous, or the *analogues* of each other. **Analogy** is the term we use when we wish to express this resemblance. It is, of course, unnecessary to add that many members are both homologous and analogous, *e.g* the ordinary foliage leaves of one flowering plant with those of another.

The student will now be able to understand the two principles referred to They are :—(*a*) members morphologically similar (*i e* homologous) may be differently modified for the performance of different functions; (*b*) members not morphologically similar may be similarly modified for the performance of the same function These principles should be kept in mind, and illustrations of them, in the following chapters, carefully noted

CHAPTER II.

GENERAL HISTOLOGY.

A. The Cell.

§ 1. **Cellular Structure of Plants.**—We have already explained (p 6) that the substance of the plant body is not homogeneous, but, in all except the lowest forms, consists of aggregations or unions of microscopic structures, called cells, each *living* cell consisting of a tiny mass of a viscid substance, called protoplasm, bounded by a distinct membrane, the cell-wall. These cells can be readily seen by teasing out the substance of a very ripe, mealy apple in water, and examining it under the microscope; also in thin microscopic sections of stems, roots, and other parts of plants (see, e.g., Figs. 19, 60). The protoplasm is the essential or living substance of a cell, and the seat of all the vital processes. The cell-wall is formed by the protoplasm, and, during the life of the cell, is added to and moulded in various ways according to the special functions it has to carry on.

The cell-walls, therefore, are to be regarded as constituting a skeleton or framework, giving support to the living substance, and firmness and strength to the whole organism. They do not, however, prevent communication between the living substance of the various cells, for the protoplasm of one cell is connected with that of others by means of extremely delicate threads passing through the cell-wall. Thus the living cells of a plant are bound together in organic union, and carry on in harmony the various processes necessary for the life of the plant.

In the lowest forms of multicellular plants, the organism consists of an aggregation of similar cells, all carrying on

very much the same functions; but in higher forms, correlated with the physiological differentiation which has taken place, there is what is called **Histological Differentiation.** In other words, many different kinds of cells, more or less definitely arranged in groups, can be recognised, the form and structure of the cells in each group depending on the functions entrusted to them. This differentiation becomes more and more marked as we pass from lower to higher types In the Thallophyta and Bryophyta, all parts of the organism consist of *living* cells, although these cells may present many different forms For this reason these two divisions are distinguished as **"cellular plants."**

A considerably higher differentiation is exhibited by the Pteridophytes and Flowering Plants, in which, owing to their adaptation to an existence on land, elaborate arrangements have been developed for the proper conduction and distribution of nutritive substances In these groups, in addition to typical living cells having an infinite variety of form, long, slender, and often tubular structures of an altogether different character can be recognised These run through the masses of cells, sometimes irregularly, more often in definite strands or bundles (see Fig 61) They are, to a large extent, structures adapted for the rapid transmission of nutritive fluids, that is, *vascular* structures

Although very different in appearance from typical cells, a study of their development shows that all these tube-like structures are really formed by the union and alteration of young cells. The Pteridophytes and Flowering Plants are distinguished by the presence of such vascular structures in their tissues, and are therefore spoken of as **"Vascular Plants."** Hence also the term *Vascular* Cryptogams for the Pteridophytes. Thus, however extensive the differentiation may be, we may say that all parts of plants are made up of cells or of structures, or *elements*, derived from cells

§ 2. **Protoplast or Energid.**—In section, the cells of a plant present a general resemblance to the cells of a honey-comb. This was the origin of the term "cell." In many ways it is misleading and inaccurate. In plants each fully formed cell or tube has its own proper wall, and by suitable methods can be isolated for indi

vidual examination. The walls of the cells in a honey-comb, on the other hand, are common walls. Again, the protoplasmic contents are the essential part of a cell. As a matter of fact, in certain stages of the life history, certain of the protoplasmic bodies have no protective membrane—*e.g.* the ovum or egg-cell and the spermatozoid. Here the term "cell" is not at all appropriate, and the case is not improved by the use of such terms as "*naked cell*," "*primordial cell*," etc. The term "cell," however, has become so fixed in the nomenclature that it is impossible to avoid using it. At the same time many botanists have now come to apply the terms "**protoplast**" or "**energid**" to any living uni-nucleated protoplasmic unit, whether enclosed in a cell-wall or not.

§ 3. **The Young Cell.**—Young cells are always found at points where growth is going on (**growing-points**)—*e.g.* at the apex of a stem. They are called initial or **meristematic** cells. They show repeated division into two, and it is in this way that new cells are produced in the plant. These young cells have very simple definite forms. They show no trace of the differentiation which in the higher types is so marked in the older parts of the plant. At the growing apex of a stem or root they are always more or less four-sided or polygonal in section (Fig. 4, A). In some meristematic regions (cambial layers, see § 20) they are elongated and flattened (Fig. 4, B)

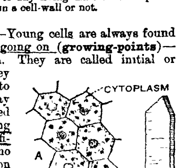


FIG 4.—A, YOUNG OR MERISTEMATIC CELLS, B, CAMBIAL CELL.

In all cases, however, the cell-walls are extremely thin, and the protoplasm completely fills the cell-cavity. The general protoplasm of the cell (as in *all* living cells) is called the **cytoplasm**. It is always more or less granular, and embedded in it are several denser and more highly specialised *protoplasmic* bodies. Of these the largest and most important is the **nucleus**. It is probably an essential constituent of the living cell, although its presence in some of the lowest forms has not yet been demonstrated. The others usually present are known as **plastids**.

§ 4 **The Cell-Wall.**—The cell-wall in young cells, and in many fully developed cells, consists of a substance called **cellulose,** with which are associated other substances known as pectic compounds Cellulose is a carbohydrate, *i.e.* it is one of a large group of organic substances, consisting of the chemical elements carbon, oxygen, and hydrogen, in which the hydrogen and oxygen are in the same proportions as in water (water = H_2O). The formula of cellulose may be given as n $(C_6H_{10}O_5)$, the value of *n* being doubtful.

Cellulose is readily recognised by the use of reagents. It is dissolved by an ammoniacal solution of cupric hydrate (Schweizer's reagent), which does not act on the pectic substances With Schulze's solution it turns blue; with iodine solution and sulphuric acid it swells up and turns blue.* The molecules of cellulose are probably arranged in groups forming particles, each invested by a film of the watery sap which permeates the cell-wall It is because of this that substances in solution in water can diffuse through the cellulose wall

§ 5. **The Protoplasmic Substance.**—Protoplasm is essentially clear and jelly-like, but often presents a granular appearance, owing to the formation of various bodies within its substance. It is an extremely unstable substance of highly complex composition, and when dead is found to consist mainly of **proteid** substances, which are highly complex compounds of carbon, hydrogen, oxygen, nitrogen, sulphur, and occasionally phosphorus, but whose exact composition has not yet been determined. Thus protoplasm contains these chemical elements in very complex proportions. Phosphorus is always present in the protoplasmic substance of the nucleus, but it does not appear to be an essential constituent of protoplasm in general.

* Schulze's solution (also known as chlor-zinc iodine) is prepared by dissolving zinc chloride, potassium iodide, and iodine, in certain proportions, in distilled water Iodine solution is best made by dissolving iodine in a solution of potassium iodide and diluting with water.

Protoplasm is coagulated by alcohol and acids, and also by heat, the temperature at which coagulation takes place varying according to conditions. Iodine solution stains protoplasm yellow, the denser forms (*e.g.* nuclear substance) brown Protoplasmic substance is dissolved by solutions of caustic potash and chloral hydrate. Like the cell-wall, all protoplasmic substance is permeated with water. The vital power of protoplasm seems to depend on the constant presence of water. From this alone the student can readily infer the essential importance of water to the life of the plant.

§ 6. **The Nucleus** is a body of the highest importance in the life of the cell. It appears to be the originating centre of all the vital processes—the initiator and director of all the cell's activities. According to some it plays an important part in connection with the nutrition of the cell. It seems, however, to exercise a special control over reproductive processes. This will be evident when we come to consider the processes of cell-division and sexual reproduction

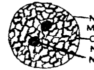


Fig 5 —Nucleus.

The nucleus (Fig 5) is bounded by a delicate **nuclear membrane** formed from the surrounding cytoplasm. Inside there is a semifluid ground-substance, the **nucleo-hyaloplasm**, in which is embedded a network of fine fibrils usually spoken of as the **chromatin network**. In the ground-substance also, lying in the meshes of the chromatin network, are to be found one or more small granular bodies, the **nucleoli**. The chromatin network and the nucleoli are the parts which take on stains most readily

Nuclei are usually spherical or oval in form, but may be flattened or more or less elongated. They are never formed "de novo," *i.e.* by the simple aggregation and differentiation of the protoplasmic substance, but always by division of pre-existing nuclei The division of the

nucleus is either *direct* or *indirect*. In the former method there is a simple splitting or bipartition, which is not accompanied by the division of the cell. This *direct* method is known as **fragmentation**; it is found chiefly in old cells which become multinucleate. In the *indirect* method a complicated series of changes is gone through which constitute what is known as **karyokinesis** or *mitosis* (see § 18). It is followed by cell-division.

§ 7 In some cells either one or two small spherical bodies have been observed lying close to the nucleus. These are called **centrospheres**. The centrospheres present in animal cells are regarded as important structures; but, in plant cells, their presence has been definitely established only amongst the Thallophyta and Muscineæ, where they are especially prominent during nuclear division. Apparently they are not to be regarded as permanent or essential structures in plant cells

§ 8. **The Plastids** (Figs 4, A and 16), like the nucleus, are highly specialised and differentiated portions of protoplasmic substance. Similarly, they are not formed "de novo," but always multiply by division (direct). The substance of the plastid has a spongy texture. There is a clear, semifluid ground-substance, in which is embedded a network of strands or fibrils of denser proteid

§ 9. **Processes of Histological Differentiation.**—In the very young or embryo plant all the cells are meristematic, but in the older plant the meristematic cells are confined to certain points or regions which are distinguished as "growing-points"—as, *e g.*, the apical cell or cells of a thallus, the apex of stem or root. This localisation arises from the early commencement of histological differentiation. The cells which are formed are gradually altered or modified in various ways to adapt them to the performance of different functions, and in this way are produced all the varieties of cell and tissue met with in the fully developed organs of a higher plant. *All these different kinds of cells or cell-structures are derived by modification of various kinds from the young cells produced at growing-points.*

Before we can satisfactorily describe these various forms and kinds of cells, we must consider the nature of the changes or modifications which give rise to them. In other words, we must give some account of the *processes of histological differentiation.* These changes affect both the cell-wall and the cell-contents. They may be roughly tabulated thus —

(1) Growth in surface-extent of the cell-wall.
(2) Thickening of the cell-wall.
(3) Chemical alteration and impregnation of the cell-wall.
(4) Changes in the contents.
(5) Cell-fusion.

§ 10. **Growth of Cell-Wall in Surface-Extent.**—In other words, the cell grows in size This growth may be uniform or localised. If uniform, the young cell simply develops into a larger cell of the same form. If localised, the resulting cells assume new forms.

If, for example, the young cell grows more especially at three or four particular points, the resulting cell will show a number of radiating arms or outgrowths (the *stellate* form—Fig 27, A). If rapid growth is confined to two opposite points the cell becomes very long and *pointed.* This elongated pointed kind of cell is very common. It is called the **prosenchymatous** form (Fig. 6), and is to be distinguished from the **parenchymatous** form, in which the cell is usually not much longer than it is broad, and is not pointed. The parenchymatous form shows considerable variety, *e.g.* it may be rounded, oval, polygonal, prismatic, tabular or flattened, stellate, etc. Localised growth in surface-extent, then, gives rise to different forms of cells.

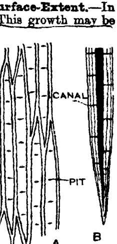


Fig 6.—Sclerenchyma (Prosenchymatous).
A, Not strongly thickened; B, End of a thickened bast-fibre.

§ 11. **Thickening of the Cell-Wall.**—The thickening of the cell-wall does not begin till the cell has reached its full size. It also may be uniform (general) or localised. In the former case the cell-wall is equally thickened all round. Strictly speaking it is rarely met with. Localised thickening is the rule. In this case only certain parts of the wall are thickened. The character of the thickening varies very much. In some cases it takes place in rings, so that we get **annular** bands formed on the inner surface of the cell-wall (Fig 7, A). In other cases the thickening is along a **spiral** line (Fig 7, B) We may imagine that this is due to the annular thickenings of the former case becoming interrupted and running into each other; as a matter of fact we find cases where the thickening is partly annular, partly spiral. If now we imagine the turns of the spiral to be arranged very closely, so that at intervals they fuse, we get the next type of thickening, the **reticulate** (Fig 7, C) Here the thickening forms a network or reticulum on the inner surface of the cell-wall.

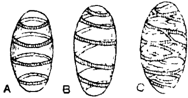


Fig 7 —TYPES OF THICKENING
A, Annular, B, Spiral, C, Reticulate

The transition from this to the **pitted** *or dotted* type of thickening (Fig 8) is easy, we have only to imagine that the strands of the network become very thick and the meshes correspondingly reduced In this case the whole of the wall, with the exception of numerous small circumscribed areas, undergoes thickening. When examined under the microscope these unthickened areas *appear* like perforations, apertures, or dots, according to their

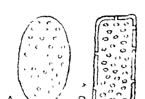


Fig 8.—PITTED CELLS
A, Surface view; B, Cell cut longitudinally, showing pits in section and surface view

size, hence the terms pitted or dotted The student should carefully notice the transition, readily recognisable, from the simple annular type to the more perfect pitted type.

The thickening substance is laid down on both sides of the original cell-wall. This, however, can generally be distinguished in the middle of the thickened wall, and is known as the **middle lamella** (Fig. 9). It is evident, then, that just as localised growth in surface-extent results in the development of different *forms* of cells, so localised thickening leads to the formation of different *patterns* or markings on the cell-wall. These markings are most characteristically and most distinctly developed on wood-elements (wood-vessels and tracheides), but are not by any means confined to these

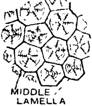


Fig 9.—Thickened Sclerenchyma. (Transverse section.)

Sometimes the thickening of the cell-wall is so extensive that the cavity is almost obliterated. This is frequently the case in the elements forming a tissue called sclerenchyma (Figs. 9, 6B) If pits are present they become transformed into canals running through the thickened wall

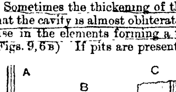


Fig 10.—The Bordered Pit
A, Longitudinal section; B, Surface view; C, Semi profile

A curious form of pit, the **bordered pit** (Fig. 10), is developed on the walls of many wood-vessels and tracheides. Here a circular area of the cell-wall remains unthickened, and the edge of the thickening matter all round this arches over it in a dome-like manner The apex of the dome, however, is open, so that there is an aperture leading from the small cavity covered over by the dome into the cavity of the tracheide or vessel. A similar structure is developed *at exactly the same point* in the adjacent tracheide or vessel.

A glance at Fig. 10, A, C, will now show that in the wall separating the cavities of the two vessels or tracheides there is a lenticular space across which stretches the original unthickened cell-membrane. In a surface view of the structure (Fig. 10, B) we see the small aperture at the apex of the dome as a small circle, surrounded by a larger circle representing the edge of the unthickened membrane where the thickening matter begins to arch over the lenticular cavity.

The student will get a good idea of this structure if he takes two small wooden dishes shaped like watchglasses, makes a perforation in the bottom of each, and places

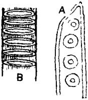


Fig 11.—Bordered Pits in Surface View
A, Circular, B, Elongated (scalariform).

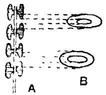


Fig 12.—Oval Bordered Pits.
A, Longitudinal section, B, Surface view.

them rim to rim with a thin sheet of paper between. The thin paper between the dishes will represent the unthickened cell-wall. It should be noticed that the thin membrane in a fully developed bordered pit shows a slight swelling or thickening in the middle, called the *torus*, and is frequently found pushed over to one side so as to close the pit.

These bordered pits are frequently met with on the walls of the wood-elements of Angiosperms and Vascular Cryptogams, but they are most typically developed on the wood-elements (tracheides) of Gymnosperms.

Sometimes the pits on a wood-element are very much elongated transversely. In this case the thickened bars between the elongated pits look like the rungs of a ladder; hence the name **scalariform**, applied to this type of

thickening. The pits in this scalariform type are frequently bordered (Figs. 11 B, 12).

§ 12. **Note.—The growth and thickening of the cell-wall** is due to the formation of new particles of cellulose by the protoplasm, and their incorporation in the cell-wall According to some, these particles are laid down in layers on the inner surface of the wall. This is the **apposition theory**. Here, increase in surface-extent is supposed to be due to stretching of the wall. Others maintain that the new particles are intercalated, or pushed in between those already present. This is the **intussusception theory**. Probably both processes go on together, apposition being more important in the case of thickening, intussusception in the case of growth in surface extent.

§ 13 **Impregnation and Chemical Alteration of the Cell-Wall.**—The thickened cell-wall may show much the same chemical characters as the young cell-wall, *i.e.* it may consist of cellulose with associated pectic substances. But, in many elements, the wall during growth becomes impregnated with various substances or altered in other ways. It may be cutinised, suberised, lignified, converted into mucilage, or impregnated to a greater or less extent with mineral matter.

Cutinisation is due to the chemical alteration of the cell-wall accompanied by impregnation with a waxy substance called *cutin*. This modification is most commonly seen in the outer layers of the external walls of epidermal cells, where it has been called *cuticularisation*. The cutinised layers extend over the epidermis, forming a membrane known as the **cuticle** (see Fig. 33, A) The properties of the cell-wall are completely altered by this change. It not only gives firmness to the walls, but also renders them almost impermeable to water.

Suberisation is a very similar modification, due to the formation of a waxy or fatty substance called *suberin*. This change is met with in cork cells, and, like cutinisation, it renders the cell-walls impermeable to water. Cutinised or corky walls are stained yellow by iodine solution, yellow or brown by Schulze's solution. They are not acted on by sulphuric acid.

Lignification was formerly ascribed to the formation in the cell-wall of a substance called lignin. More probably it is due to chemical alteration of the cell-wall and its impregnation with various substances It is met with only in thickened cell-walls, as in the cells or elements of wood and sclerenchyma While giving great strength and rigidity to the cell-wall, this change does not interfere with its elasticity or permeability. Lignified walls are stained a bright yellow by aniline sulphate (or chloride), yellow, or sometimes brown, by iodine, yellow by Schulze's solution; under the action of iodine and sulphuric acid they become brown and swell up *

Mucilaginous walls, when dry, are hard and horny. The property which peculiarly distinguishes them is their great capacity for absorbing water. When moistened or soaked in water they swell up and become soft and sticky This property of absorbing and retaining water is of use to plants which are exposed to periods of drought or risk of desiccation. In extreme cases the absorption of water may lead to the disorganisation of the mucilaginous cell-wall, and produce drops of gum This is the origin of the exudation of gum seen on the stems of cherry and other trees, also in many bud-scales. The process of germination is facilitated in various seeds, *e g.* the Flax, because, owing to the mucilaginous character of the cell-walls of the seed coat, the seed readily adheres to the soil Mucilage, chemically, is closely allied to cellulose, of which it may be regarded as a modification.

Of the mineral substances deposited in the cell-wall silica, calcium carbonate, and calcium oxalate are the commonest. Silica is often found so completely impregnating the cellulose wall that if the tissue is burned a complete siliceous skeleton of the cells is left behind, *e g.* in the epidermal tissues of grasses. Isolated crystals of calcium oxalate or, less frequently, of the carbonate are occasionally found in cell-walls. The distinguishing test for these

* See footnote, p. 22. Aniline sulphate solution is a saturated solution of aniline sulphate in water, to which a drop of sulphuric acid is added.

mineral substances is dilute acetic acid. Calcium oxalate does not dissolve in this acid: but calcium carbonate does, with an evolution of gas (CO_2). Both are acted on by hydrochloric acid.

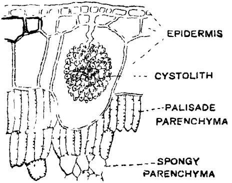


Fig 13.—Part of Transverse Section of the Leaf of *Ficus elastica* (Indiarubber Plant), showing a Cystolith

The most interesting form in which calcium carbonate is associated with the cell-wall is that known as the **cystolith** (Fig. 13). Cystoliths are found only in a few plants, e g the epidermal cells of plants belonging to the Nettle order and of the India rubber Plant. During their development a small cellulose protuberance arises on the cell-wall internally As the protuberance grows, it becomes impregnated with calcium carbonate When fully developed the cystolith forms a pear- or cigar-shaped mass, attached by a short stalk to the cell-wall. It has an organic basis of cellulose.

§ 14. **Changes in the Contents.**—In the young cell, as we have seen, the protoplasm, etc., completely fills the cell-cavity As the cell grows the increase in the amount of protoplasm is not sufficient to keep pace with the extension of the cell-wall The result is that small spaces or cavities, called **vacuoles** (Fig. 14), make their appearance in the protoplasm. They are filled with a watery fluid called **cell-sap**. In the very young cell the relatively small amount of cell-sap simply permeates the protoplasmic substance and the cell-wall.

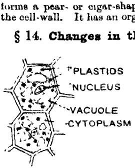


Fig 14.—Young Cells showing Formation of Vacuoles

These small vacuoles gradually increase in size, and finally all run together to form one large central vacuole (Fig. 15). The protoplasm is now reduced to a **parietal layer**, which lines the cell-wall internally, and a number of delicate **protoplasmic strands** or threads which run across the vacuole to the middle of the cell. The parietal layer forms a sort of bag containing the cell-sap. Hence, when first seen, it was called the "**primordial utricle**," a name which is still in use.

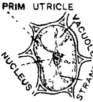


Fig. 15.—A Typical Living, Fully Developed Cell.

The nucleus in such a cell is embedded in the little central mass of protoplasm formed by the union of the protoplasmic strands, but it lies in the primordial utricle when, as frequently happens, the protoplasmic strands are absent. This condition of the cell is met with in many fully developed plant-tissues, *e.g.* the general succulent tissue of plants.

In young cells the **plastids** are colourless. They multiply by *direct* division (Fig. 16), and during the growth of the cell they may undergo many changes as regards colour. It is only in the older living cells of the plant that they attain their full functional activity. Three kinds are differentiated.

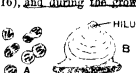


Fig. 16.—Plastids (highly magnified).
A, Chloroplasts of a Moss (*Funaria*), showing division; B, Leucoplast with developing Starch-Grain.

In the cells of underground portions of plants (*e.g.* tubers of Potato), or deep-seated tissues (*e.g.* medullary rays of trees)—more generally in tissues not exposed to light—they are colourless and called **leucoplasts** or **amyloplasts**. They have various forms—spheroidal, discoidal, rodlike, etc. Their special function is the formation of starch from soluble carbohydrates (sugar).

In parts exposed to light, such as leaves and the superficial tissues of herbaceous stems, most of the plastids develop the green colouring matter called **chlorophyll.** They are therefore called **chloroplasts, chlorophyll corpuscles,** or chlorophyll grains. The chlorophyll is apparently dissolved in an oily fluid which permeates the protoplasmic substance of the plastid.

The function of chloroplasts is twofold. Like the leucoplasts they can form starch from soluble carbohydrate, but in addition to this, by means of the chlorophyll which they contain, they have the power of building up carbohydrate substance from water and carbon dioxide in the presence of light (see p. 13). In all the higher plants they are spherical or spheroidal, often more or less flattened. Sometimes the green colour is masked or concealed by the presence of other colouring matters dissolved in the cell-sap, *e.g* leaves of the Copper Beech When exposed to light leucoplasts develop into chloroplasts, while the latter lose their chlorophyll and become yellow if withdrawn from light

Frequently, however, the plastids in aerial parts contain colouring matters other than green. Such are called **chromoplasts.** They are found in the petals of many flowers—most yellow and many red flowers—and in fruits. The colours of most blue flowers and many red flowers, on the other hand, are due to colouring matters dissolved in the cell-sap Chromoplasts may be formed directly from leucoplasts, but usually from chloroplasts. Thus the young floral leaves may be green, and the colours of autumn leaves are due to the presence of chromoplasts derived from chloroplasts by the decomposition of the chlorophyll towards the approach of winter

The colours of chromoplasts are due to the presence of colouring matters known as xanthophyll (yellow) and carotin (orange-red). Chromoplasts sometimes assume crystalline forms owing to the crystallisation of carotin, *e g* in the cells of the root of the Carrot. Chloroplasts and chromoplasts are called **chromatophores** (colour-bearers)

Many **non-living substances** may be produced during the metabolism of the cell, and are found either in the

protoplasm or in the cell-sap. These substances are either soluble or insoluble. In the former case they are dissolved in the cell-sap; in the latter they appear in solid form, usually in the protoplasm. They may be arranged in three groups. First, there are **plastic substances** which are at some time or other made use of by the protoplasm as food-material (see p. 15). The most important are starch grains, proteid grains (Fig 17), oil or fat (these are insoluble), various sugars and nitrogenous compounds of the nature of amides (these are soluble). Then there are **secretions** (p. 15). The more important are the organic acids, various colouring matters, and many ferments (these are soluble).

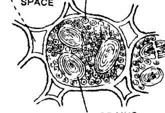


Fig 17.—Cells with Grains of Starch and Proteid.

The third group consists of those substances which, being of no apparent use to the plant, are called waste-products or **excretions**. The most important are the alkaloids. These are nitrogenous substances, many of which constitute the active principles of medicinal plants, *e g.* morphine, atropine, quinine, nicotine, strychnine, caffeine, etc. Amongst the waste products are also included ethereal oils, resins, tannins, and various mineral substances.

Some of the more important non-living substances mentioned above will be considered more fully in § 17 It must be pointed out here, however, that there is no clear distinction between these three groups of substances. As illustrating this point reference may be made to a large group of substances found in plants. They are called *glucosides*, and may be regarded as compounds of glucose or grape-sugar with various nitrogenous and non nitrogenous substances. Of these amygdalin, found in the Almond, coniferin in Conifers, salicin in Willows, are examples. They are generally included amongst the waste-products. When acted upon by ferments, however, they are decomposed, and glucose, a nutritive

substance, is usually one of the products. Thus the glucosides might equally well be regarded as stored plastic compounds.

Take another example. We have already referred to the mucilaginous modification of cell-walls. But mucilage may also be found amongst the cell-contents, and is sometimes poured into special tubes or ducts. It is found in many plants which have to make provision for water-storage, *e.g* the bulbs of Onion and of various Orchids, the leaves of many succulent plants, etc. Since it enables plants to store up water it may be regarded as a secretion product. On the other hand there are certain cases in which mucilage must be regarded as a storage form of food-substance, as in the seeds of certain Leguminosæ. With regard to substances usually classified as waste-products our knowledge is limited. It may be that many of them play an important part in the metabolism of the plant

Finally, in connection with the changes taking place in the interior of cells, it has to be noticed that the contents, protoplasmic or otherwise, disappear altogether from many cells towards the close of their development. Evidently the tissues consisting of such "cells" can only discharge a purely mechanical or physical function as vascular or supporting tissues. Here the cell-walls are of importance, not the living substance. The protoplasm ends its work when it has sufficiently moulded the walls in accordance with the functions they have to carry on, and disappears. The occurrence of tissues which have lost their living substance and are therefore dead must be carefully noticed We have examples of these in wood-vessels and sclerenchyma (Figs. 6, 9).

§ 15 **Cell-Fusion.**—Frequently, in the development of masses or rows of cells, the cell-walls break down and disappear. The extent to which this takes place varies considerably. Sometimes a whole mass of cells disappears owing to complete absorption and disappearance of their walls, and a large irregular space or cavity is formed This is the origin of most of the large irregular cavities met with in plants, such, for example, as the spaces found in the middle of many stems.

Sometimes more definite passages are formed by a similar absorption of longitudinal series of cells. Cavities or passages formed in this way, by complete absorption of

cells are said to be developed **lysigenously** (Fig. 18). On the other hand, definite tubes or **vessels** *bounded by distinct walls* are produced from rows of cells, if the absorption affects only those walls which lie between the original cells, so that their cavities become continuous. If

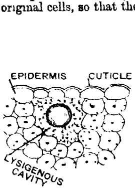


Fig 18 —LYSIGENOUS CAVITY WITH DROP OF ETHEREAL OIL.

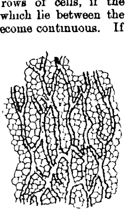


Fig 19 —LATICIFEROUS VESSELS RUNNING THROUGH THIN WALLED PARENCHYMA.

irregular rows of cells fuse in this way, the vessels formed branch and anastomose (*i e.* the branches run into each other) to form a network, as in the formation of laticiferous vessels (Fig 19) A straight, tubular vessel is formed if cells in a single definite longitudinal series fuse together, as in wood-vessels (Fig 61).

§ 16. **Intercellular Cavities.**—Young cells are all closely in contact with each other There are no spaces between them. But, in cells growing in different directions and taking on different forms, the cell-walls must be subjected to a considerable amount of strain. The cell-walls yield to this by splitting at certain points, so that small cavities, called *intercellular spaces*, appear between the cells. In most cases these are small, and, *in sections*, are seen more especially at the angles of the cells (Figs 15, 17). They are not, however, isolated from each other, but communicate so as to form a continuous system. They are of

great importance in the plant, as they serve for the ready passage of various gases and vapours, the most important of which are oxygen, carbon dioxide, and water vapour

Frequently larger cavities or passages are formed by the *separation* of masses of cells from each other, owing to a splitting apart of the cell-walls in this way. This is the **schizogenous** method of development of such spaces and passages. Most **resin-passages**, *e g.* Ivy, Scots Fir, are formed in this way.

§ 17. **Non-living Cell-Contents.**—We must now give a fuller account of some of the more important non-living substances found in cells, and already mentioned on p. 33.

(1) **The Cell-Sap** is a watery fluid, containing many substances either in solution or in suspension. The water is derived from the soil in the process of root-absorption. It contains various inorganic salts, nitrates, sulphates, phosphates, etc., dissolved in it. Amides (*e g.* asparagin, $C_4H_8N_2O_3$) and sugars are the most important plastic substances contained in the cell-sap. The chief sugars are grape-sugar ($C_6H_{12}O_6$) and cane-sugar ($C_{12}H_{22}O_{11}$).

Another carbohydrate sometimes found is inulin, a form of starch. **Inulin** is especially abundant in the cells of many Compositæ (*e g.* roots of Sunflower and Dahlia). Though dissolved in the cell-sap, it is precipitated by alcohol in the form of very characteristic crystalline masses, called *sphærites* (Fig 20), marked by a series of concentric and radiating lines.

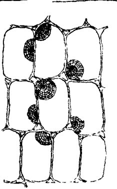


Fig. 20.—Cells with Inulin-Crystals

Colouring matters, organic acids (*e.g.* malic, citric, tartaric, and oxalic), and ferments are the most important of the secretions present. As already mentioned, excreted products such as tannin, glucosides, and various alkaloids are also present.

The cell-sap is to be regarded as a nutritive fluid and as a receptacle for waste products It can diffuse from cell to cell, and permeates the substance of protoplasm and cell-wall, so that the protoplasm absorbs from it the substances necessary for its nourishment

(2) **Starch** is a carbohydrate and an isomer of cellulose, i e. it contains the same chemical elements in the same proportions, but has a different chemical constitution, so that its properties are different Its formula may be given as $n\ (C_6H_{10}O_5)$. It is found in plant-cells in the form of grains (Figs. 17, 21), most abundantly in parts which serve as store-places of reserve material

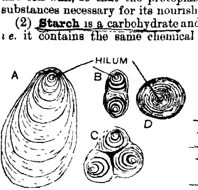


FIG 21 -- STARCH GRAINS.
A, Excentric, D, Concentric B, C, Compound

Rarely the grains are formed in the general protoplasm of the cell; in this case they are small and devoid of any structure Their formation is nearly always the work of leucoplasts, chloroplasts, or chromoplasts They are developed inside the plastids, and chloroplasts are often much distended by them. The starch grains present in chloroplasts are small because there the storage of starch is temporary In the case of leucoplasts, which are found in more permanent store-places, they are frequently large, and appear to lie outside the plastids, owing to their formation beginning near the margins of the plastid bodies (Fig 16)

When the grains are examined under the microscope they are found to exhibit stratification, a number of layers being arranged round a definite point called the **hilum**. Sometimes the layers are arranged quite regularly and concentrically (Fig. 21, D), but often the arrangement is excentric, and the hilum lies near one end (Fig. 21, A). Concentric grains are formed in the centre of the plastids; excentric grains to one side of them. The reason, of

course, is that, in the former case, the substance of the plastid invests the grain equally, and regular starch-layers are deposited; while, in the latter case, the starch-layers are thickest on the side next the main body of the plastid.

The starch-grain contains water. The stratified appearance is due to splits appearing in the substance of the grain owing to contraction. The regions where splitting occurs are rich in water. Starch grains usually also contain a gummy substance, *amylopectin*, which causes the grains to unite when treated with boiling water. The grains assume many different forms, but the form is characteristic in each particular plant. Those of the Potato are oval or ovate and excentric; of the Wheat, spherical or lenticular and concentric; of the Rice, polygonal.

Sometimes a plastid begins to form a number of grains at the same time. As these grow they are enclosed in common layers and form compound grains (Fig. 21, B, C). Spuriously compound grains are produced by separate grains simply becoming aggregated together. Starch-grains when fully formed may be found floating free in the cell-sap. Starch is stained a dark blue, sometimes violet, by iodine solution, and is therefore readily detected.

(3) **Proteid Grains** (Figs. 17, 22). These are solid grains of proteid substance formed as reserve food-material in connection with nutrition. They are formed from vacuoles, whose contents, rich in albumen, harden into grains. They may be found in any living cell, but are especially large and abundant in the cells of many oily seeds. In many cells they are extremely minute and form granular aggregations. They are spoken of generally as **aleurone grains**.

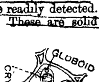


FIG. 22.—CELL WITH LARGE ALEURONE GRAINS.

If some of the larger forms met with in seeds (*e.g.* Castor Oil or Brazil Nut) be examined, they are found to contain a denser proteid body called the **proteid crystalloid** (Fig. 22), and also,

to the side of this, a clear mineral body, called the **globoid,** consisting of a double phosphate of calcium and magnesium. Sometimes a number of crystalloids are present in an aleurone grain. The grains, especially the crystalloids, are stained yellow or brown by iodine (cf. the nucleolus and chromatin fibrils of the nucleus). By taking on stain in this way, and also by the fact that it can be made to swell up under the action of various reagents, the crystalloid is readily distinguished from a mineral crystal.

Aleurone grains are insoluble in alcohol, but are more or less soluble in water or in a solution of salt Proteid crystalloids are not present in all proteid or aleurone grains, and they may occur by themselves, as in the outer cells of the potato-tuber, and in the seed of the Brazil Nut

(4) **Fats and Oils.**—Fatty oils occur in the form of drops or globules in the general protoplasm of cells and also in the vacuoles, and are found most commonly in seeds, *e.g.* sweet oil in Olive, linseed oil in Flax. They may be considered, chemically, as compounds of glycerine and fatty acids. All of them are soluble in ether, but, with the exception of castor oil, almost insoluble in alcohol They are non-volatile and are obtained from seeds by pressure. Most of them are stained brown by 1 per cent solution of osmic acid.

(5) **Resin** appears in various forms in many cells, sometimes mixed with other substances such as tannin, gum, or mucilage Frequently the resin is poured into special resin-passages

(6) **Ethereal or Essential Oils** occur frequently, as excretions (or secretions), in the vegetative parts of plants, *e.g.* in the cells of many leaves, and in glandular hairs They belong to various groups of chemical compounds and are quite distinct from the fatty oils They differ also from the fatty oils in being volatile Owing to this they leave no permanent mark or stain on paper and can be prepared by distillation. Like the fatty oils, however, they are stained by osmic acid. They may serve a useful purpose in plants by warding off insects, and the odours of flowers, which attract insects, are due to the presence of ethereal oils in the petals.

(7) **Mineral Crystals.**—Both the oxalate and the carbonate of lime are precipitated in the form of crystals or crystalline masses. They may be regarded as excretions of superfluous mineral matter. The oxalate is by far the commoner. They may occur in the form of small crystals (Fig. 23), or in rounded and more or less angular crystal-

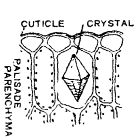


Fig 23.—Part of Transverse Section of a Leaf (Region of the Upper Surface), showing a Crystal in one of the Cells.

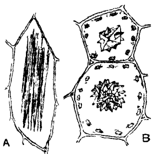


Fig 24.—Cells with A, Raphides; B, Sphæraphides.

line aggregates called **sphæraphides** (Fig. 24, B). A very characteristic form of calcium oxalate is the elongated acicular or needle-like form Groups of these acicular crystals occur in the cells of many Monocotyledons (*e g* Arum) and some Dicotyledons (*e.g.* species of Dock) They are called **raphides** (Fig. 24, A).

§ 18. **Cell-formation.**—Having described plant-cells, their structure, modifications, and contents, we have now to consider the origin or formation of new cells, for it is evident that wherever growth or reproduction is taking place there must be development of new cells. In all cases new cells are formed from pre-existing cells. In the vegetative parts of plants they are nearly always produced by very characteristic **cell-division.** Each meristematic cell, after reaching a certain size, divides into two daughter-cells, which may repeat the process. The division of the cell is preceded by the karyokinetic division (p. 24) of the nucleus.

Sometimes in vegetative parts, but more frequently in connection with reproductive processes, new cells are developed by a process known as **free cell-formation**, in which also there is karyokinetic nuclear division. In the development of reproductive cells, two other processes are met with, in which there is no preceding nuclear division—namely **rejuvenescence** and **conjugation**. We shall now briefly consider these methods of cell-formation

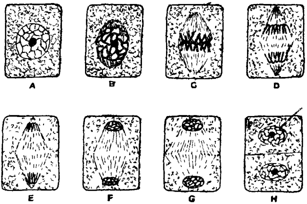


Fig. 25 —Stages in Karyokinesis and Cell division.

(1) **Ordinary Cell-Division.**—Here we have to describe the series of changes which take place in the indirect division of the nucleus and constitute **karyokinesis** or **mitosis** (see Fig 25) First the nucleus becomes larger; then the chromatin network thickens, opens out into a convoluted thread, and finally breaks up into a number of curved U- or V-shaped rods called **chromosomes**. The number of these is constant for each species of plant. During these changes the nuclear membrane gradually disappears, and a number of fine fibrils or threads are formed in the surrounding cytoplasm, giving rise to a barrel-shaped structure called the **nuclear spindle** (A-C) The chromosomes pass to the equator of the spindle and

attach themselves to its threads with their free ends directed outwards. They thus give rise to a star-like structure called the **nuclear disc** (C). This is the *star* or *aster* stage in the process. While the nuclear disc is being formed each chromosome divides *longitudinally* into two thinner Us or Vs, so that the number of chromosomes is doubled. Then the chromosomes begin to move along the threads of the nuclear spindle outwards to the poles—half of them to one pole, the other half to the other pole. In this movement the apices of the V-shaped chromosomes are directed outwards (D, E). It should be remembered that the two halves of each original chromosome pass to opposite poles. In this way the substance of the original nucleus is equally divided. At the end of the movement we can recognise two stars; this is the *diaster* stage.

At each pole the chromosomes become aggregated, and thus two **daughter nuclei** are formed (F-H). During the process of nuclear division the nucleoli are disorganised, nucleoli reappear in the daughter nuclei. In the lower plants centrospheres (p. 24) have been observed at the poles of the spindle; they appear to act as directive centres.

Towards the close of nuclear division, when the daughter chromosomes are passing outwards to the poles, small granules are deposited on the threads of the nuclear spindle in the equatorial region. These fuse to form a membrane called the **cell-plate.** During its formation the spindle threads increase in number so that the new membrane extends laterally until it reaches the walls of the parent cell (F, G) The cell-plate then splits into two layers, and the new cell-wall which divides the mother cell into two daughter cells is laid down between them (H). This primary cell-wall, after thickening takes place, persists as the *middle lamella* (p 27), and usually consists, not of cellulose, but of some pectic substance (calcium pectate).

Since, in the process of nuclear division, each chromosome divides into two, it is evident that the daughter nuclei contain the same number of chromosomes as the parent nucleus. This is always the case in connection with the formation of vegetative cells. But

an interesting modification of the process occurs in the first division of the mother-cells which give rise to the spores in the higher plants The convoluted thread formed from the chromatin network when nuclear division is beginning is really *double*, owing to the union of the chromosomes in pairs. The V-shaped segments into which it splits are therefore paired chromosomes, and, in the formation of the daughter nuclei, these simply separate from each other.

There is thus no division of the individual chromosomes, and the daughter nuclei present in the spores contain only half as many chromosomes as the parent nucleus. This is known as the reduction division or the reduction of the chromosomes. All the cells derived by division from the spores have this reduced number of chromosomes. It is evident, however, that in the life-history of the plant there must be a stage at which the chromosomes are doubled This occurs at the time of fertilisation (see p. 45).

(2) **Free Cell-Formation.**—This type of cell-formation differs from the above in that division of the cell does not *immediately* follow mitotic division of the nucleus. By repeated mitotic division of the successive daughter nuclei, a large number of nuclei are produced lying free in the protoplasm of the cell. Towards the close of this process the protoplasm begins to aggregate round these nuclei to form naked protoplasts (p 20) Finally, cell-walls are formed between them. These new cells are formed *inside* the mother-cell, and the young cell-walls are entirely new structures. In ordinary cell-division the dividing plate is the only *new* part of the cell-wall formed. Typical free cell-formation is seen in the development of the endosperm of seeds

Occasionally the rapid division of the nucleus is not followed by the actual division of the protoplasm and the formation of cell-walls. We simply get a number of nuclei lying in the protoplasm, or rather, perhaps, an aggregation of protoplasts with their nuclei. Such a structure is called a **cœnocyte.** We have examples in laticiferous "cells." The cœnocyte may seem to be indistinguishable from a multi-nucleate cell. As points of difference, it should be noted that a cell becomes multinucleate only in an old condition, and the division of the nucleus is direct, not mitotic.

(3) **Rejuvenescence and Conjugation.**—Many reproductive bodies, either asexual or of the nature of gametes (p. 16), are simply naked protoplasts, either motionless, or moving by means of vibratile protrusions of the protoplasm called *cilia*. The cells in which they are developed are called mother-cells. In many cases they are produced, not by the division of the protoplasmic contents of the mother-cells, but by a process of rejuvenescence, in which only one is formed in each mother-cell. In the process the protoplasm or part of the protoplasm aggregates in the middle of the cell, the cell-wall bursts, and the protoplasmic unit is set free, forming a new cell (protoplast) which has altogether different activities and different properties from the cell which produced it. The protoplasm has, as it were, taken on a new lease of life. Hence the term *rejuvenescence* for this form of cell-formation. It will be noticed that there is no nuclear division, and no increase in the number of cells.

A similar process takes places in connection with the formation of spores in the higher plants, but in this case cell-walls are formed round the spores before they are set free

Conjugation is the term applied to the fusion of gametes (see p 16) Not only the protoplasm of the gametes, but also their nuclei, fuse together, and the result is a new cell (zygote) with altogether different potentialities. It will be seen that, in this form of cell-formation, there is a fusion of nuclei and a reduction in the number of cells. The term conjugation is strictly applied to the fusion of *similar* or undifferentiated gametes, when the zygote is called a **zygospore.** The term **fertilisation** is given to the process in the higher plants where a *male* gamete makes its way, or is carried, to a distinct *female* gamete (**ovum** or oösphere), and the zygote is called the **oöspore.**

B. The Tissues.

§ 19. **A tissue** may be defined as an aggregation of similar cells or elements, united from the first, governed by the same laws of growth and development, and having

therefore a similar structure adapted to the performance of the same function. The significance of the differentiation of tissues has already been indicated. The tissues of a plant may be arranged in two chief groups :—(*a*) **Meristematic Tissues**; (*b*) **Permanent Tissues.** The former are the tissues found at growing-points. They consist of meristematic cells, *i.e.* cells which possess the power of dividing. In the latter group are included all tissues derived from the former by various processes of differentiation. They consist of cells or elements which have lost the meristematic property, and taken on some fixed or permanent structure, adapted to the performance of some special function.

§ 20. **Meristematic Tissues.**—As already indicated (p 24), the regions of meristem become restricted. These meristematic regions may be apical (**apical meristems**), as at the apices of stems and roots, where they provide for the further growth of these members in length But frequently we find meristematic layers situated between masses of permanent tissue (**intercalary meristems**) When an intercalary meristem provides for secondary increase in thickness of a member (the trunks of trees, for example) it is called a cambial layer or **cambium**.

Meristems are also distinguished as **primary** or **secondary**. A meristem which has persisted throughout the growth of a member (*e.g.* stem or root), and which therefore was present at the first origin of the member, is a primary meristem. So also any meristematic layers which have been *directly* derived from it, as in *parts* of some cambial layers. A secondary meristem is produced when living cells of permanent tissue take on meristematic activity. This is the case with most cambial layers.

The structural characters of meristematic cells (Fig. 4) have already been described (p. 21) We may summarise the characters of the tissue thus :—A meristem is an active growing tissue. Its cells are in an active state of division. The cells have all approximately the same form and structure. In apical meristems they are usually more or less polygonal; in cambial layers they are usually

flattened and more or less elongated. The cell-walls are thin and consist of cellulose (with associated pectic compounds); the protoplasm completely fills the cell-cavity; the nucleus is large and well-defined; there are no intercellular spaces.

§ 21. **Permanent Tissues.**—Some of these are clearly marked off from each other; but others are connected by so many transitional or intermediate forms that it is impossible to classify them sharply. As a matter of fact very different classifications have from time to time been proposed. The following classification is based partly on the forms of the component cells (parenchymatous or prosenchymatous), partly on the characters of their walls or contents (cutinised, lignified, etc.).

§ 22. (1) **Thin-walled Parenchyma** (see Fig. 60).—This is one of the commonest kinds of tissue found in plants. It constitutes the greater part of the soft succulent tissue, *e.g.* the tissue of Algæ and Mosses, the cortex and pith of stems, the mesophyll of leaves. The cells are parenchymatous in form. They may be rounded or oval, with numerous intercellular spaces (spongy parenchyma, Fig. 13), slightly elongated and arranged perpendicularly to some surface (palisade parenchyma, Fig. 23), elongated and prismatic, stellate, etc., etc. The thin cell-walls consist of cellulose. Primordial utricle, protoplasmic strands, nucleus, vacuole, and cell-sap are usually present. Various substances may be formed in the cells, such as starch, proteid grains, oil, resin, etc., etc. Small intercellular spaces are nearly always present. Sometimes, as in the pith of some trees, the cells entirely lose their contents.

It is a tissue essentially engaged in the processes of assimilation and nutrition. The cells containing chlorophyll can elaborate organic substances; other cells serve for the storage of these substances; and, through it, plastic substances in solution in the cell-sap are carried by slow diffusion over the whole plant. Although the cell-walls are comparatively thin it also exercises a strengthening or supporting function by reason of the turgid condition

of the cells. The important part it plays in this respect is shown by the drooping of herbaceous plants when deprived of water.

Occasionally a similar tissue, but consisting of more or less prosenchymatous cells, is met with. This may be distinguished as **thin-walled prosenchyma.** There is, however, no sharp distinction between parenchyma and prosenchyma.

§ 23 (2) **Thick-walled Parenchyma.**—In this tissue also the cells are parenchymatous and retain their contents, but the cell-walls are more or less thickened. The thickened walls may consist of cellulose, as in the tissue called **collenchyma** (Fig 26) In collenchyma the cellulose thickening is laid down more especially at the angles of the cells; it is a tissue found underneath the epidermis of many stems and leaf-stalks. In other forms of thick-walled parenchyma the walls are not only thickened (equally), but also lignified, as in many of the thick-walled elongated parenchymatous cells of the wood (**wood-parenchyma**).

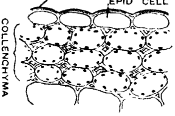


Fig. 26 —EPIDERMIS AND COLLENCHYMA OF STEM OF SUNFLOWER (Transverse section.)

The cells of collenchyma contain chloroplasts; the wood-cells usually contain storage products. But in addition to nutritive or assimilatory functions, this tissue has a mechanical function, giving strength to the parts in which it occurs. Collenchyma is usually found in members which are still growing

Occasionally **thick-walled prosenchyma** is met with. The cells may be unlignified (*e.g.* some bast-fibres), or lignified. The protoplasmic contents are always small in amount. The cells may be spoken of as fibrous cells, or, if lignified, fibrous sclerotic cells.

§ 24. (3) **Sclerenchyma** (Figs. 6, 9).—Amongst the thin- and thick-walled tissues just described there are many transitional forms. Similarly the thick-walled lignified forms lead up gradually to the tissue called sclerenchyma. In this tissue the contents have been completely lost, and the walls of the elements are thickened and lignified. Its function in the plant is purely mechanical. It is the chief strengthening tissue found in plants, and its distribution in stems, leaves, and roots is largely determined by the strains to which these members are subjected. Frequently the thickening of the walls is so great that the cavities are almost obliterated (Fig. 9).

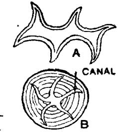


Fig 27 —SCLEROTIC CELLS.

Sclerenchyma usually and typically consists of prosenchymatous elements (**fibrous sclerenchyma**). These elements are often referred to as **sclerenchymatous fibres.** This form of sclerenchyma is typically developed in bands or bundles (**stereid bundles**) The hard bast of most fibro-vascular bundles is a good example of this (see Fig 61) Occasionally, however, sclerenchyma consists of rounded or slightly elongated parenchymatous elements Such **sclerotic cells** (Fig. 27), as they are called, are found in some fruits (*e g.* the "stone cells" of the Pear), and in the cortex and secondary phloem of some woody stems, *e.g.* the Oak

The sclerenchymatous elements as a rule have simple pits on their walls. If the wall becomes very strongly thickened, these pits are converted into elongated, often branching, canals (Fig. 27, B). Practically it is convenient to regard all thickened forms of prosenchyma as sclerenchyma.

§ 25. (4) **Cutinised or Suberised Tissue.**—In this tissue the cell-walls are cutinised or suberised (p. 29), partially or completely. It is met with in various parts of plants The cells are parenchymatous in form, usually either flattened and tabular or more or less brick-shaped.

The best examples of this kind of tissue are seen in the **epidermis** of stems and leaves, in **cork**, and in the **endodermis** or bundle-sheath of roots

In the epidermis, only the outermost layers of the external walls are cutinised, forming the **cuticle** (p. 29 and Fig 26). Cork consists of more or less brick-shaped cells without intercellular spaces Frequently the walls are comparatively thin, but examples of thick-walled cork cells are abundant The walls may be suberised throughout, and the older cork cells lose their contents. Endodermal cells may be thin, or, as frequently happens, certain of them are more or less thickened.

The function of the tissue is protective—more especially to prevent evaporation or diffusion of watery fluids.

§ 26 (5) **Tracheal Tissue.**—This is the essential tissue of the *xylem or wood* In it we recognise two kinds of elements —(*a*) **Wood-vessels** (vasa or tracheæ, Fig 61); (*b*) **tracheides** (Fig. 11, A). In both of these the walls are thickened and lignified, and the protoplasmic contents have disappeared. In both, annular, spiral, pitted, or scalariform patterns may be developed on the walls. The tracheide, however, is a prosenchymatous element developed from *a single cell*; whereas the vessel is a long, tubular structure derived by *cell-fusion* from a longitudinal row of cells

In the Angiosperms the vessels are the characteristic structures of the wood, although tracheides also are found, especially in the secondary wood of Dicotyledons. Wood vessels vary in length from a few inches to a yard, or in some cases more. In Gymnosperms and Vascular Cryptogams there are, with rare exceptions, tracheides only. Tracheal tissue is usually found in bundles

Owing to the thickening and lignification of the walls this tissue performs a mechanical or supporting function, but it is specially adapted to discharge a vascular function. It is essentially a vascular tissue It serves for the rapid transport of watery solutions from the root, where they are absorbed, to the leaves and other organs, where they are elaborated

A typical sclerenchymatous fibre is distinguished from a typical tracheide in that, having only a strengthening function, it is more completely thickened, and shows no large or definite pattern, like the tracheide. Transitional forms, however, are of common occurrence.

§ 27. (6) **Sieve-tube Tissue** (Figs. 28, 29).—This is the essential tissue of the *phloem* or *bast* (soft bast) of vascular bundles. **Sieve-tubes** are typically developed in the Angiosperms. In this group they are long, slender structures composed of elongated cells placed end on end. The walls are thin and consist of cellulose. The end-walls are specially thickened and modified to form **sieve-plates**, the structures characteristic of sieve-tubes. In the thickening of these end-walls small areas remain thin, forming pits. The thin membranes closing these pits are ultimately absorbed (p. 35), so that the end-wall is actually perforated in a sieve-like manner, and the contiguous cells are placed in communication.

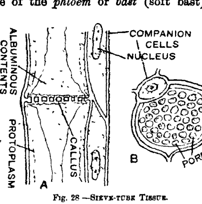


Fig. 28.—Sieve-tube Tissue.

A, Longitudinal section of a sieve-tube through a simple sieve-plate, B, Transverse section showing the sieve-plate in surface view.

Usually the whole of the end-wall is perforated in this way to form a simple sieve-plate (Fig. 28). Frequently, however, when the end-wall is not horizontal, but obliquely inclined, we can recognise on it a number of areas perforated in this way, the whole structure forming a compound plate (Fig. 29). Less frequently in Angiosperms the sieve-plates are formed on the lateral walls.

Inside the sieve-tubes there is a lining layer of protoplasm, but no nuclei. The protoplasm is continuous through the pores of the sieve-plate, and at the sieve-plate there is frequently deposited a peculiar substance called **callus.** Callus is abundantly developed in the autumn, sometimes to such an extent that the pores of the sieve-plate are completely stopped up (*e.g.* in the Vine). The contents of the sieve-tubes (in addition to the protoplasm) are albuminous. This albuminous substance is found more especially aggregated in the region of the sieve-plates; it contains small starch grains, and, owing to the presence of these, is stained slightly violet or purple by iodine

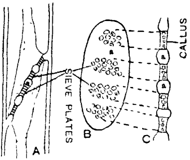


Fig 29 —SIEVE-TUBE TISSUE—COMPOUND SIEVE-PLATES

A, Longitudinal section, B, Oblique compound plate in surface view, C, in section a — thickened portions of the wall between the sieve-plates.

Along with the sieve-tubes in Angiosperms are thin-walled elongated **companion cells**, so called because they are closely associated with the sieve-tubes, from which they are cut off during development.

Structures similar to the sieve-tubes of Angiosperms, consisting of elongated prismatic cells, are found in Gymnosperms and Vascular Cryptogams Their sieve-plates are, however, most abundantly developed on the lateral walls and the perforations are small They contain no starch. It should be noticed also that sieve-tubes, or structures closely resembling sieve-tubes, are found in some of the larger Algæ where there is a rudimentary development of vascular or conducting tissue.

Sieve-tube tissue discharges a vascular function. It serves for the *rapid* transport of elaborated food-material to the various parts of the plant.

§ 28. (7) **Laticiferous Tissue (Milk-Tubes).**—This is a tissue found only in certain groups of plants. It consists of long, branching tubes, containing a characteristic substance, often milky in appearance, and called **latex.**

Two kinds of laticiferous tissue are recognised. The first kind consists of **vessels** formed by cell-fusion. Owing to the fact that the fusion takes place, not in definite longitudinal rows of cells, as is the case in wood-vessels, but in irregular series, the vessels not only are branched, but anastomose (*i.e.* the branches run into each other) to form a network (Fig. 19). The second kind consists of **cœnocytes** (p. 44). In the embryo of a plant which possesses these, certain peculiar cells can be recognised. In development these "cells" elongate and branch, but transverse septa are not formed in them There is, however, repeated karyokinetic division of the nucleus, so that these structures are not elongated branched cells, but cœnocytes. Seeing that there is no cell-fusion, it is evident that the branches of these cœnocytes do not anastomose (Fig 30).

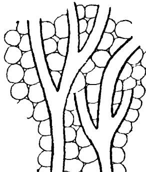


Fig 30—Laticiferous "Cells" (Cœnocytes) of Euphorbia, running through thin-walled Parenchyma

In both vessels and cœnocytes the walls are somewhat thickened, but consist of cellulose; there is in both a lining layer of protoplasm with nuclei. Laticiferous vessels are found in many Compositæ (*e g.* Dandelion), Papaveraceæ (*e g.* Poppy), and Campanulaceæ (*e g.* Harebell) Laticiferous cœnocytes are found very typically in the Spurges (*Euphorbia*), Urticaceæ, Moraceæ, and others.

The contained substance, the **latex,** presents different appearances in different plants. It is rarely quite watery

(Banana), usually it is more or less milky (*Euphorbia*), occasionally thick and coloured (in *Chelidonium majus*, the Greater Celandine, a plant allied to the Poppy, it has an orange colour). It consists of water containing various substances, either in solution or in suspension. These substances are usually of the nature of excreted products, so that the tubes are often to be regarded simply as reservoirs of excreted matter. Of such substances opium, guttapercha, caoutchouc, tannins, resins, and gums are examples

Frequently, however, the tubes contain nutritive substances as well. These may be nitrogenous or non-nitrogenous. The latex of *Euphorbia*, for example, contains elongated, rod-shaped or dumbbell-shaped starch-grains. To some extent, therefore, laticiferous tissue may discharge a vascular function, serving for the storage and transport of nutritive substances.

The latex, in many cases, is poisonous, and in contact with the skin causes irritating sores, so that it no doubt often serves for protection by warding off the attacks of enemies.

§ 29 (8) **Glandular Tissue.**—This tissue consists of structures of various kinds in which secreted or excreted substances are produced. Many of these have been spoken of as "secretion reservoirs" Although laticiferous tissue has been treated by itself, it is not clearly marked off from this glandular form of tissue. The substances produced are of very varied character, such as gum, mucilage, resin, tannin, ethereal oil (Fig. 18), mineral crystals (Figs 23, 24), water, etc

Single cells ("sacs") containing such substances are frequently found scattered here and there through the tissue of plants—*e g.* tannin or resin cells, cells containing raphides, etc. These are examples of **idioblasts**, *i.e.* isolated cells, which differ from the surrounding cells either in structure or in contents.

Cells active in the secretion or excretion of water constitute organs which have been called **hydathodes.** The water, which is poured out on the surface, often contains mineral

substances, such as carbonate of lime, in solution, *e g.* in Saxifrages. The hydathode may consist of a group of epidermal or sub-epidermal cells, or it may take the form of epidermal hairs

Closely allied to hydathodes are the multicellular glands forming the nectaries of flowers, the digestive glands of insectivorous plants, and the extrafloral nectaries which are found on the leaves and other members of various plants, *e g.* on the leaf of the Cherry A **nectary** consists of a group of epidermal and sub-epidermal cells; the sugary secretion is poured out on the surface and serves to attract insects to the flower. The function of **extrafloral nectaries** is not understood. By some it is believed that they attract small insects and so keep them away from the flowers; by others, that they supply food to various insects which are of use to the plant in that they attack and destroy others which are injurious.

Glandular hairs and other glandular epidermal structures must also be noticed here (epidermal glands). The hairs may be unicellular or multicellular. The secretion may be formed in any of the cells of a multicellular hair, but is usually found in the terminal cell, which is frequently more or less dilated or globular The mucilage or resin produced in many winter buds (*e g.* the Horse Chestnut) is formed by hairs of this kind.

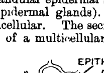


Fig 31 —Resin-Passage. (Transverse section)

Finally, the "secretion-reservoirs" may be of the nature of cavities or passages formed either lysigenously or schizogenously (pp. 36, 37). Lysigenous cavities, containing various kinds of ethereal oils, are frequently found in leaves (Fig. 18) and also in many fruits (*e g* orange and lemon) Most **resin-passages** (Fig. 31) are examples of such structures formed schizogenously. The resin-passage is usually surrounded by a layer of small thin-walled parenchymatous cells—the **epithelial layer**—by which the substance poured into the passage is formed.

C. Tissue-Systems.

§ 30. In plant-members the various forms of permanent tissue which we have just described are aggregated in various ways to form higher unities called **tissue-systems.** In all the higher plants there are three systems which, from their constant appearance in roots, stems, and leaves, stand out clearly and constitute systems of the first rank These are (*a*) **the epidermal system,** (*b*) **the vascular system,** (*c*) the system of the **ground- or fundamental tissue.** It will be advisable to give a short general account of these before going on to consider the various arrangements met with in different types

§ 31 **The Epidermis—general characters** (Figs. 32, 33) —The epidermal system, or epidermis, is the outermost *protective* layer or membrane of stems, roots, and leaves. In many cases, as will afterwards be explained, a *true* epidermis is wanting altogether, its function being often taken on by the outermost layer of ground-tissue As aerial stems and leaves are the members most exposed to adverse external influences, it is on these that we naturally find the highest development of the epidermal system

Typically an epidermis consists of cutinised tissue (p 49), forming a single layer of cells. Sometimes it consists of several layers. This is the case at the apex of most roots where the many-layered epidermis forms a protective structure called the root-cap (Fig 77) An epidermis of several layers is also found in a few stems and leaves. For example, in the leaf of the Indiarubber Plant (Fig 13) it consists of three layers of small cells, with here and there a larger cell containing a cystolith, and serves, apparently, as a tissue for the storage of water In the epidermis of aerial parts we find *ordinary epidermal cells, stomatal* or *guard-cells,* and various *epidermal outgrowths.*

§ 32. **The ordinary epidermal cells** of a typical one-layered epidermis are always more or less flattened or tabular. Their outline, when seen in surface view, is very various. As a general rule, however, in *long* members they are considerably elongated in the direction of the length of the member, *e g.* stems and many monocotyledonous leaves (Fig. 32, A), while, in members as broad or nearly

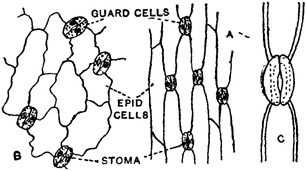


Fig 32.

Epidermis of (A) Monocotyledonous leaf (Iris), B, Dicotyledonous leaf (C) Stoma of Iris (a small outer cavity to the stoma is indicated by the dotted line)

as broad as long, they are not elongated, but have an extremely wavy outline, *e g.* most dicotyledonous leaves (Fig 32, B).

As already indicated (p. 29), the outer layers of the external walls are cutinised to form the protective cuticle, which serves to prevent undue evaporation from the tissues and ward off the attacks of insects and Fungi. Frequently also the cuticle is covered with a thin layer of wax ("bloom"), which prevents the surface being wetted and retards the giving off of water vapour The cuticle and waxy bloom are most strongly developed in plants which live in bright sunlight (sun-plants), or in dry places, or which have for various other reasons to economise their water supply and guard against the risk of desiccation. In shade- and moisture-loving plants the cuticle is poorly

developed and it is absent from roots and the submerged parts of aquatic plants.

In most Flowering Plants, the ordinary epidermal cells, although they usually have protoplasmic contents, contain no chloroplasts. The meaning of this is apparent if we remember that chlorophyll is decomposed by exposure to bright sunlight. In aquatic plants, however, and in many shade-loving plants, including Ferns and other Vascular Cryptogams, chloroplasts are present in these cells.

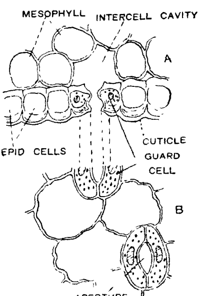


Fig 33.—EPIDERMIS AND STOMATA. A, Section; B, Surface view

§ 33. **Guard-Cells and Stomata.**—The stomatal or guard-cells are so called because they surround or guard the openings, known as stomata (Figs. 32, 33), numerously developed in the epidermis of aerial parts. These stomata communicate with the system of intercellular spaces in the underlying ground-tissue, and serve, as we shall see later, as a means of gaseous interchange between the plant and the atmosphere.

Usually each stoma is surrounded by two guard-cells—one on each side The guard-cells are crescentic in form. They always contain protoplasm, nucleus, and numerous chloroplasts. Their walls are thickened; the thinnest in each guard-cell is that which is farthest from the pore

The guard-cells can alter their form, and thus increase or diminish the size of the opening. In this way they have an important part to play in regulating the amount of water-vapour passing out of the plant in the process of transpiration. Sometimes other small cells (*subsidiary cells* of the stoma) lie outside the guard-cells.

In the development of a stoma, a small cell, the mother-cell of the stoma, is cut off from a young epidermal cell. A cell-wall then divides the mother-cell into the two guard-cells. The opening or stoma is formed by the splitting of the common wall between the guard-cells. Subsidiary cells, when present, are formed by the division of the surrounding epidermal cells.

§ 34. **Position of Stomata.**—Stomata may be developed on all *aerial* leaf and stem structures—even on the ovary and anthers of the flower. They occur on the spore-capsules of many Bryophyta, but with this exception they are confined to the Vascular Cryptogams and Flowering Plants They are not developed on roots or aquatic members. On green foliage leaves, where they are most numerously developed, their number and position depend largely on the position and direction of the leaf, and on the conditions with regard to transpiration. In bifacial leaves (p. 11) they are usually most abundant on the lower surface, sometimes confined to it, as in most evergreens, which have to guard against excessive transpiration On floating leaves, *e.g.* leaves of the Water Lily, they are found on the upper surface. In some bifacial leaves, but more especially on vertical leaves (isobilateral leaves, *e.g* the Iris), they are about equally distributed on both surfaces.

§ 35. **Epidermal Outgrowths.**—Frequently there are outgrowths of the ordinary epidermal cells. These are of the nature of hairs or **trichomes** (Fig. 34). They are of varied character—sometimes unicellular, sometimes multicellular. They may end in a sharp point (*spike-hairs*), or in a rounded knob (*capitate hairs*). They may be membranous and attached by their surface to the epidermis (*scale-hairs*). Elongated membranous hairs

attached by one end are called *ramenta*. The hairs may be *branched*. In many cases they are *glandular*.

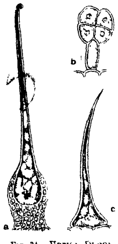


Fig 34 —URTICA DIOICA (NETTLE)

a, Stinging hair, b, Multicellular glandular hair, c, Ordinary unicellular pointed hair (Highly magnified)

Their function is chiefly protective. Thus a thick covering of hair is developed on many plants growing in dry situations, and diminishes transpiration. Glandular hairs protect plants against the attacks of insects. The stinging hairs found in the Nettle and other plants discharge a protective function in a more aggressive way. **Root-hairs** are absorbing organs, *they are always unicellular.*

The stinging hair of the Nettle (Fig. 34a) has a siliceous point which is readily broken off When a nettle is touched by the hand, the point breaks and a little wound is made in the skin, into which the acid sap is forced by the sudden contraction of the base of the hair.

Emergences.—Stronger outgrowths are often found on the surface of the plant. They differ from trichomes in containing a core of ground-tissue (occasionally also vascular tissue) and not being outgrowths of the epidermis alone. Such outgrowths are called emergences. Frequently they are of the nature of **prickles**, as *e.g.* in the Rose (Fig. 88) Other examples are found in the *membranous* outgrowths, called **ligules**, of many leaves, *e.g.* the leaves of Grasses (Fig. 86, E), the petals of the Pink (Fig. 122, B).

§ 36. **Water-Pores or Water-Stomata.** — Other openings, closely resembling stomata in appearance, but differing from them in important respects, are frequently found on leaves, *e g* in Fuchsia and Garden Nasturtium. They are called *water-pores* or *water-stomata*, because, instead of giving out water-vapour, they excrete drops of water. They are on the average larger than stómata, and their guard-cells, having lost their protoplasmic contents, have no power of altering their shape They are usually developed in groups on the upper surfaces of leaves, frequently on leaf-teeth or leaf-apices These groups are often found over the fine terminations of the veins of the leaf, *i e* the terminations of the vascular system, and are associated with a peculiar glandular tissue

(*epithem tissue*) which is found at the ends of the veins. This glandular tissue is a form of *hydathode* (p. 54) The water which is excreted sometimes contains calcium carbonate, as in Saxifrages. In this case the glands have been called *chalk-glands*.

§ 37. **The Vascular System.**—This is the system of tissue which serves for the rapid transference of nutritive fluids in the plant. Typical vascular tissue is found only in the Vascular Cryptogams and Flowering Plants (p. 20). It is *a continuous system in stem, leaf, and root* Usually it consists of a varying number of strands or bundles—**vascular bundles**—running longitudinally through stem and root, and passing out into the leaves at all levels. These bundles consist of parts (made up of various tissues) called **phloem (soft bast)** and **xylem (wood)**. In stems and roots showing secondary increase in thickness owing to the activity of a cambium (p. 46), as in trees, this primary arrangement in bundles is modified, and stout cylinders of phloem and xylem are produced. At present, however, we shall confine ourselves to the general characters of a vascular bundle

§ 38. **The Vascular Bundle** (*e.g* Figs. 60, 61, 70, 79).—Vascular bundles may consist of xylem only, or of phloem only, as in roots; or, as in stems and leaves, of both xylem and phloem. In the latter case they are called **conjoint bundles.** The xylem essentially contains tracheal tissue (p. 50). Associated with this, however, there are parenchymatous cells (either thin-walled or thickened and lignified—p 48) called **wood-parenchyma,** and frequently also sclerenchymatous fibres, called **wood-fibres.** The phloem essentially contains sieve-tubes (p. 51), but associated with it is a certain amount of thin-walled parenchyma—consisting, in Angiosperms, of companion cells (p. 52), and usually, also, of other cells known as *phloem-parenchyma*

Attached to the outer side of the phloem in many bundles there is a bundle of fibrous sclerenchyma, This, which is a strengthening tissue, really belongs to the ground-tissue, although it is called the **hard bast.** The phloem tissue is distinguished from this as the **soft bast.**

When a bundle contains a marked amount of sclerenchymatous tissue, or has a stereid bundle (p. 49) associated with it, it is called a **fibro-vascular bundle.**

At the apex of stem or root the bundles pass into the meristematic tissue, from which they are differentiated. In the leaves they spread out and form the veins; the veins end in various ways

§ 39. **The Ground-tissue System** includes all tissues not belonging to the epidermal or vascular systems It is evident, therefore, that it consists of many different kinds of tissue, and has many functions to discharge The most abundant tissue is thin-walled parenchyma; but associated with this are the other tissues in varying amount—sclerenchyma, collenchyma, laticiferous tissue, and glandular tissue. Very frequently this system is marked out into distinct regions, such as the *pith*, the *cortex*, the *medullary rays*, the *hypodermis*, the *endodermis* or bundle-sheath, the *pericycle*. All these will be described in due course.

PART II.—THE ANGIOSPERM.

CHAPTER III.

SEED AND EMBRYO.

§ 1 Before proceeding to a detailed consideration of the form and structure of the various members of the adult plant, it will be advisable to examine their earliest forms as found in the embryo This is readily done by studying the structure and germination of a few seeds. The study is essentially a practical one and must be carried out by the student himself. The following descriptions and figures, therefore, are merely intended to help and direct him in his work.

§ 2 **The Sunflower* Seed** (Fig. 35).—The so-called Sunflower seeds are really fruits, each containing one true seed. They were attached to the parent plant by the pointed end. Before examination they should be soaked in water for some time. The wall of the fruit is called the pericarp and can readily be removed by means of a penknife. The seed which lies inside is invested by

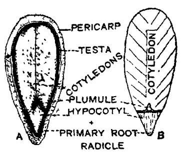


Fig 35 – Fruit and Seed of Sunflower. A, Longitudinal section of fruit; B, Embryo with one cotyledon removed.

* *Carthamus tinctorius* (Kusum) may be substituted, and is exactly like the Sunflower.

a thin yellowish or brownish membrane, constituting the seed-coat and called the **testa**. The removal of this discloses a rather fleshy embryo plant, pointed at one end. The pointed end is called the **radicle**. The greater part of the embryo above the radicle can readily be split into two lobes. These are called the **cotyledons**, and are thick and fleshy because of the large amount of stored food-material which they contain.

If a thin section of a cotyledon be examined under the microscope, the embryonic cells can readily be made out. They are filled with large numbers of rounded grains, which are stained brown or yellow by iodine, and are therefore recognised as proteid or aleurone grains. A large amount of oil also is present which can be recognised, in sections mounted in water, in the form of bright, refractive globules If the cotyledons be gently separated there will be found towards the base, and lying between them, a small pointed structure known as the **plumule**. The various parts of the embryo can also be examined in a longitudinal section (Fig 77).

Germination.—If the fruit be placed in the soil, under proper conditions, the seed begins to *germinate* (Fig 36) Under the term germination are included all changes that take place from the time the dry seed is placed in proper conditions until it establishes itself The young plant in the dry seed is alive but dormant, and the germination of the seed is simply the awakening of the young plant to active life and growth.

The process can readily be studied in the Sunflower if the fruit be placed for some days in moist sand or sawdust The conditions necessary for germination are moisture, access of air, and heat. Water is absorbed and causes the embryo to swell and burst open the pericarp A certain degree of heat is necessary to start and continue the process of growth. Air is necessary for respiration, which is active in germinating seeds.

The embryo grows and develops into a seedling plant. This growth takes place at the expense of the food-material (oil and proteid grains) stored up in the cotyledons. These insoluble food-substances are rendered soluble by

means of ferments (p 34); they are, in fact, converted into soluble compounds by a process of digestion. The soluble compounds diffuse to the growing apices of the plumule and radicle, and are made use of as food-material by the protoplasm.

During these changes the pericarp and testa are split open at the pointed end. The tip of the radicle first elongates and makes its way out of the fruit (Fig 36, A). It grows downwards into the soil, and forms the root. The part of the radicle immediately beneath the cotyledons, known as the **hypocotyl**, also elongates, and grows upwards, carrying with it the cotyledons, which increase in size, turn green in the sunlight, and are then readily recognisable as *leaves* of very simple form. The *plumule*, which is at first concealed between the cotyledons, eventually develops into the stem and leaves of the Sunflower plant.

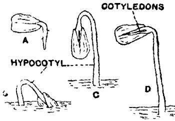


FIG 36 —GERMINATION OF SUNFLOWER SEED

When it first appears at the surface of the soil the hypocotyl has the form of a loop or arch (Fig. 36, B) The advantage of this in overcoming the resistance of the overlying soil, and in preserving the plumule and cotyledons from injury, is obvious. The empty fruit-coat may be left behind in the soil, but is usually carried above ground on the tips of the cotyledons (Fig 36, D). The *hypocotyl* is the portion of the axis which, after germination, lies between the cotyledons and the surface of the soil. As we shall see later, it is intermediate in structure between stem and root

From the above it is evident that the plumule must be regarded as the embryonic *shoot*, the cotyledons as the embryonic *leaves*, and the radicle as the embryonic *root* (and hypocotyl). In the Sunflower, as in most seeds, the plumule is an extremely small conical structure, showing

no trace of young leaves. In some plants, however, it is large (*e.g.* the Almond), and bears little outgrowths which are easily recognised as tiny undeveloped leaves. The axis of a plumule is called the epicotyledonary portion of the axis, or simply the **epicotyl**. *Together* with the radicle it constitutes the axis of the embryo, just as stem and root constitute the axis of a full-grown plant.

In the Sunflower there are two cotyledons. This is characteristic of the *Dicotyledons*, the group of Angiosperms to which the Sunflower belongs. When the cotyledons come above ground and form the first green foliage leaves of the plant, they are said to be **epigeal**. This is the case in most dicotyledonous flowering plants.

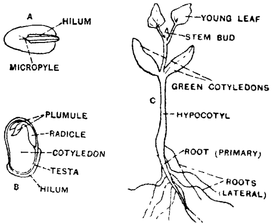


Fig 37.—SEED AND EMBRYO OF LABLAB.
A Entire, B, One cotyledon removed, C, *After germination (reduced).*

§ 3 **Seed of Lablab or of Pea** (Fig 37).—This is a true seed, and is contained in the pod or fruit. The seed, as before, should be soaked first in water, so that the **testa** or seed-coat may be easily removed. On the testa at one end of the seed there is an elongated, narrow, whitish scar, the **hilum**. This is the point where the seed has broken away from its stalk. On gently pressing the

soaked seed, a drop of moisture will be seen to exude from a minute aperture—the **micropyle**—situated at one end of the hilum. Hilum and micropyle are present, but not easily recognisable in the Sunflower.

Inside the seed-coat there is a large embryo plant. This consists, as in the Sunflower, of a radicle, a plumule, and two cotyledons. The **radicle**, which is seen to one side, lying in a little pocket formed by the seed-coat, is short and blunt. Its tip lies close to the micropyle. The **cotyledons** here are much more massive than in the Sunflower, because of the larger amount of food-material stored up in them The food-material consists of starch and proteid grains. The **plumule**, as in the Sunflower, lies between the cotyledons. It is, however, larger, and shows the rudiments of young leaves

A striking difference between the Pea and Sunflower is found in the behaviour of the cotyledons at germination. In the Pea the hypocotyl remains short, and the cotyledons do not come above ground, but remain inside the seed-coat, and simply supply food-material to the young plant. Such cotyledons are said to be **hypogeal**. This is the case in a number of plants where the cotyledons are massive The plumule escapes from the seed-coat owing to the elongation of the stalks of the cotyledons The arched form of the epicotyledonary portion of the axis should be compared with that of the hypocotyl in the Sunflower

The structure and germination of the Lablab should be compared with that of its allies, the Pea (*Pisum sativum*), Ground-nut (*Arachis hypogæa*), Broad Bean (*Vicia Faba*), Crab's Eyes (*Abrus*), Lima Bean (*Phaseolus lunatus*), and Gram (*Cicer*) In the case of the first three the cotyledons are hypogeal, while in the remainder they are epigeal.

§ 4. **Castor Oil Seed** (Fig. 38).—Seeds of the Castor Oil Plant (*Ricinus communis*) should be obtained from a seedsman The hard shell of the seed is the *testa* or seed-coat At one end of it there is a little mass, which swells up in water. This is called the *aril*; it is an outgrowth on the seed coat

On cutting a longitudinal section of the white body which is obtained on removing the testa, it is found that it contains an embryo consisting of plumule, radicle, and two cotyledons The radicle is distinctly marked, and lies towards the end where the aril is The plumule is small, and is found, as in the Sunflower, between the cotyledons The cotyledons are thin and membranous, and are completely surrounded by a white substance, which forms the greater part of the contents of the seed The latter is a tissue containing a store of food-material, and is known as the **albumen*** or **endosperm**. If the endosperm tissue be pressed against a sheet of paper a greasy mark is produced, which indicates the presence of oil The oil can be recognised in the form of globules if sections of the endosperm be mounted in water. The cells of the endosperm also contain large aleurone grains

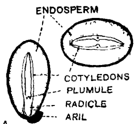


Fig 38 – SEED OF CASTOR OIL. A, Longitudinal section, B Transverse. The dark outline is the testa

Thus in the seed of the Castor Oil the food-material is contained in a special tissue in which the embryo is embedded. Seeds of this kind are called **albuminous** or **endospermic.** In the Sunflower and Pea food-substance is also stored up, but it is in the cotyledons, and not in a special layer of endosperm tissue. Such seeds are **exalbuminous** or non-endospermic.

In the process of germination the cotyledons of the Castor Oil remain for some time inside the seed. They absorb the food-material in the endosperm and increase in size Owing to the elongation of the hypocotyl the seed is carried above ground and the cotyledons form the first green leaves As in the Sunflower the hypocotyl is bent or arched when it reaches the surface of the soil

* The term albumen here must not be regarded as indicating any definite chemical compound. It came to be applied in this connection by *analogy* with the albuminous white substance in a hen's egg.

§ 5. **Maize.**—The so-called Maize seed is really a fruit containing a seed. *Pericarp* and *testa* are both thin, and fused together to form a single membrane. The grains of the "White Horsetooth" variety are larger and more regular in shape than those of the ordinary "Indian Corn," and are therefore better for purposes of study. The seeds may be softened before examination by soaking them in hot water for some time.

On one side of the fruit there is an oblong area of a light colour (Fig 40, B). The embryo lies immediately underneath this. If the fruit be cut longitudinally through the

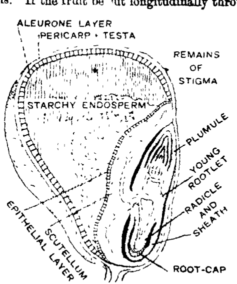


Fig 39.—Fruit of Maize cut longitudinally.

middle of this area, the embryo will be seen in section lying to one side of a mass of endosperm (Figs. 39, 40 c). When the cut surface is moistened with iodine solution, the endosperm is stained blue, and is thus shown to be rich in starch. In microscopic sections, however, it is found that the outermost layer of the endosperm, the layer lying just

under the testa, contains aleurone grains; it is called the **aleurone layer.**

The embryo consists of a large *plumule*, a *radicle*, and a single massive *cotyledon*, called the **scutellum**, which lies against the endosperm. The parts of the embryo can be recognised by dissecting the embryo away from the endosperm, but their structure is best seen in a longitudinal section under the microscope. Both radicle and plumule are large and are enclosed in sheaths

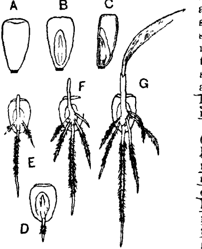


Fig 40 —Germination of Maize
A, B, Fruit in surface view, C, Fruit in section, D G, Stages in development of seedling

At germination (Fig 40) the scutellum or cotyledon remains behind in the seed and absorbs the endosperm, *i.e* it is hypogeal. The ferment which converts the starch into sugar is secreted by the cells of the outermost layer, the **epithelial layer**, of the scutellum (Fig 39) The radicle passes down into the soil and may give off lateral branches It does not, however, give rise to the root-system of the plant. It is replaced by roots which are developed from the base of the stem, and which can be recognised in a rudimentary form on the embryo even before germination begins (Fig. 39)

The plumule passes above ground, and very soon the first foliage leaf unfolds During its growth it bursts its sheath, which can be seen surrounding the base of the first leaf (Fig. 40, G) By some this sheath is regarded as the cotyledon; according to this view the scutellum is simply

an absorbing organ developed from the axis of the embryo. It should be noticed that the plumule in the Maize, being pointed, readily pierces the overlying soil; it therefore does not form a loop or arch, but grows straight through.

The "seeds" of the Rice and the Sorghum should be compared with that of the Maize. Their form is different, but their structure and germination are essentially the same. These plants belong to the group of the **Monocotyledons**, in which, as the name indicates, the embryo has only one cotyledon or seed-leaf.

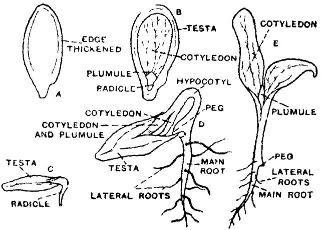


FIG 41.—GERMINATION OF GOURD.
A, Seed. B, Seed with one cotyledon removed. C, Beginning of germination D, E, Further stages

§ 6. **Notes on other Seeds.**—The four seeds described above may be regarded as examples of the more important types of seed. The following, which are considered more briefly, should be compared with them:—

The Gourd.—The seeds are flattened with a thickened margin; they are exalbuminous, the embryo having two rather fleshy cotyledons, which usually show the leaf-veining on their inner surface (Fig 41). The testa when wetted becomes sticky, thus helping to anchor the seed to its place of germination. The radicle and

plumule are short and comparatively thick. If the seed be laid flat and germinated, a peg is formed on the hypocotyl, which holds the seed-coat open for the escape of the plumule. The cotyledons are epigeal.

The Coffee (Fig 42, A–C) —The two seeds are enclosed in a scarlet berry-like fruit, usually known to coffee planters as the cherry. They are flattened, and have a longitudinal groove on the sides facing one another, and are enclosed in a slimy substance the innermost layer of which is parchment-like. The seed chiefly consists of hard horny endosperm, and the small embryo is embedded in its lower end, on the side remote from the groove. It may readily be seen by carefully shaving away the endosperm. The two cotyledons

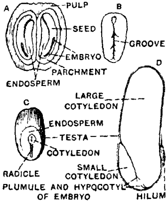


Fig 42 —Coffee and Jak

A, Coffee fruit cut in half B and C, Seed of Coffee, in C, endosperm cut away, exposing embryo D, Seed of Jak, cut in half

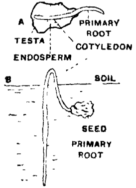


Fig 43

Germination of Onion.

are small and rounded, generally with five well-marked veins. The radicle is relatively long, and curved more or less parallel to the surface of the seed. The reserve material consists of thickened cell-walls, oil, and proteid grains. The germination is extremely slow, lasting several weeks; this is probably owing to the hard character of the endosperm. The cotyledons are epigeal.

The Jak (Fig 42, D) —The Jak fruit is composite, being formed from the whole inflorescence, the seeds are numerous, and are embedded in a fleshy pulp. The fruit, which is very heavy when fully grown, hangs, not upon a twig of the general branching system of the tree, but upon a twig which appears as an adventitious bud upon the main stem. Outside the seed is a brown seedcoat, in which two layers may easily be distinguished, the inner one being

the darker. The embryo is exalbuminous and the greater part of the seed is filled by the cotyledons, which are unequal in size, and exude latex when cut. The hypocotyl and plumule are well marked. The cotyledons are hypogeal They become green inside the seed-coat, but never come above ground, the first part of the young plant to appear being the plumule.

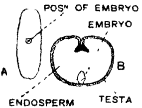


Fig. 44.—A, Seed (Stone) of Date; B, Transverse Section through Embryo.

The Onion (Fig 43).—The small black seeds are very irregular in shape, but are somewhat pointed at the base where the seed was attached to the fruit. Before examination the seed should be soaked in water to soften it. A longitudinal section should show a somewhat slender curved embryo embedded in endosperm The radicle is towards the pointed base of the seed; towards the other end is the single cotyledon. The plumule is small and is concealed within the base of the hollow cotyledon.

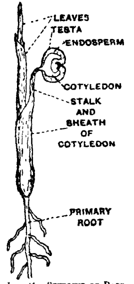


Fig 45.—Seedling of Date. The seed ("stone") is shown in transverse section.

At germination the radicle elongates and grows down into the soil as the first root, but afterwards, as in the Maize, its place is taken by roots developed from the base of the stem The lower part of the cotyledon also elongates and grows out of the seed-coat Bent over so as to form a loop or arch like the hypocotyl of the Sunflower, it passes above ground and forms the first green foliage leaf. The tip of the cotyledon, however, remains coiled up inside the seed-coat for the purpose of absorbing the endosperm. At a later stage a second leaf, developed from the plumule, bursts through the base of the cotyledon and comes above ground.

The Date (Figs. 44, 45) —The familiar Date "stone" is the seed. The brown outer layer is the seed-coat. Along one side there is a deep groove or furrow. In the middle of the other side a little protuberance will be observed, which marks the position of the embryo. If the "stone" be cut across transversely at this point, the little embryo will be seen embedded in hard, horny endosperm. The

hardness of the endosperm is due to the thickness of the cell-walls, which represent a store of carbohydrate food-material in the form of cellulose.

The process of germination can be studied if the stone be put in moist sawdust or soil and kept sufficiently warm, *e g* in a hot-house The pointed radicle elongates, grows down into the soil, and forms the primary root The lower part (sheath and stalk) of the single cotyledon also grows out of the seed, but the upper part remains inside the seed to absorb the endosperm. The cellulose is gradually converted into sugar by means of a ferment secreted by the cotyledon. The primary root branches, and is more strongly developed than is usual in Monocotyledons, but it does not give rise to the root-system of the plant. The plumule is enclosed in the sheath of the cotyledon; it bears leaves, which eventually break through the sheath and come above ground.

The Canna.—The Canna has a monocotyledonous seed, the embryo being straight, the cotyledon short and rounded. The remainder of the seed is filled with endosperm and perisperm. The cotyledon behaves exactly as in the Date, absorbing the food from the endosperm and perisperm, and passing it on to the growing parts of the seedling.

§ 7 Monocotyledonous and Dicotyledonous Seeds.

(A) *Dicotyledons* —The embryo has almost invariably two cotyledons In exceptional cases there may be three (*e g.* occasionally in Sycamore and Oak) or only one (*e g* Lesser Celandine) The seeds are in most Dicotyledons exalbuminous If the cotyledons are small and contain a relatively small amount of food-material, *e g* in Cress and Mustard, it is evidently necessary that the seedling should establish itself as quickly as possible In this case the radicle elongates rapidly and the cotyledons and plumule are quickly carried above ground by the elongation of the hypocotyl. It is only in some seeds, where the cotyledons are very large, that the latter remain inside the seed-coat, *i e.* are hypogeal

There are, however, many examples of albuminous seeds, *e g* in plants belonging to the Orders Ranunculaceæ and Umbelliferæ The amount of endosperm varies. Sometimes it is abundant, and the embryo very small. In other cases, *e g.* in Labiatæ, it is reduced to a thin layer and the embryo is relatively large. The relation of the embryo to the endosperm also varies. It may, for example, be embedded in the endosperm, or may be coiled round it.

But in all cases the tip of the radicle lies close to one side, near the micropyle. In albuminous seeds the cotyledons remain inside the seed till the endosperm is absorbed and then form the first green leaves.

Typically in Dicotyledons the primary root persists and forms the root-system of the plant

(B) *Monocotyledons.*—The embryo, as already indicated, has only one cotyledon. The seeds of Orchids and of many aquatic Monocotyledons are exalbuminous; but the great majority of monocotyledonous plants have albuminous seeds.

The cotyledon may come above ground as the first foliage leaf, as in the Onion. In most cases, however, it is hypogeal, either the whole of it, as in Grasses, or its upper part, remaining behind in the seed-coat to absorb the endosperm. Usually the radicle and plumule are pushed out of the seed by the downward growth of the lower part of the cotyledon. The plumule may be large, as in Grasses (*e g.* Maize), but it is usually very small, and, as a rule, concealed within the base of the cotyledon. The primary root, although it may develop fairly strongly at germination, is soon replaced by other roots developed from the base of the stem.

§ 8 **Uses of Cotyledons.**—From the seeds examined it will be observed that the cotyledons have various functions to perform. In nearly all cases they are concerned with the feeding or nursing of the embryo plant. In exalbuminous seeds they contain more or less food-material, and in some cases, *e g.* Oak, Broad Bean, and Pea, are food stores and nothing more. In albuminous seeds they function as absorbing organs. They secrete the ferments by which the stored substances are digested and rendered soluble and then absorb the soluble products and pass them on to the plumule and radicle. Finally in some Monocotyledons and in the great majority of Dicotyledons they form the first foliage leaves, and become active in the assimilation of fresh supplies from outside. They have a much simpler form than the foliage leaves which follow them.

§ 9. **Examination of Seeds.**—In examining seeds the student should endeavour to make out the following points:—(*a*) whether dicotyledonous or monocotyledonous; (*b*) whether albuminous or exalbuminous; (*c*) the position and form of the embryo, relation to endosperm, etc.; (*d*) the nature of the food-material stored up. Much may be done, especially if the seeds are large, by simple dissection, with the help of a hand lens. But frequently, and especially in small seeds, recourse must be had to microscopic sections. For various reasons the appearances presented by these will often be very puzzling. The embryo is often curved or folded; the cotyledons may be folded in various ways, in albuminous seeds the embryo is variously situated in relation to the endosperm. These are difficulties for which the student must be prepared.

The nature of the food-material can be recognised by applying the usual tests (for starch, proteid, oil, and cellulose). It is worth remembering that oily seeds usually contain no starch. The student therefore may expect to find starch, oil, or cellulose associated with proteid in greater or less amount.

The practical study of germination also is important. The seeds may be placed in boxes in moist sand or sawdust. A good plan is to replace one side of the box with a plate of glass and put the seeds close to the glass. Failing this a large glass jar may be lined internally with blotting-paper and then filled with moist sawdust, or, better, with bog-moss (*Sphagnum*). The seeds should be put between the glass and the blotting-paper.

CHAPTER IV

THE STEM OF THE ANGIOSPERM

§ 1 The stem and leaf structures into which the shoot in the Angiosperm is differentiated show an immense variety of forms For this reason it will be convenient to study them separately The present chapter is therefore devoted to the stem—its general external characters and internal structure

A External Characters

§ 2 **Nodes and Internodes** —We have already stated that the plumule grows upwards into the sunlight and develops into the leaf bearing stem of the plant As growth goes on the stem not only produces members unlike itself the leaves but may also give rise to similar members i e it may branch In the fully grown part of most stems the leaves are separated by intervals from each other The points at which one or more leaves are given off are called the **nodes** of the stem, and the regions between these the **internodes** (Fig 46 A)

§ 3 **General Descriptive Terms** —Usually stems in transverse section are circular, and are described as **cylindrical** Others are marked by alternate ridges and furrows, and are said to be **angular** Thus the stem of the Tulsi (*Ocimum*) is quadrangular or square. Some stems are flattened In rarer cases we meet with globular or altogether irregular stems The stem may be either **herbaceous** or **woody**. In some plants, as in the Wall flower, it is herbaceous above and woody below Some herbaceous stems are more or less dilated or expanded at the nodes. This is due to the arrangement of vascular tissue at these points. The stems appear jointed and hence the terms **jointed** or **articulated** applied to them Such stems are called **culms**. Examples

are met with in the Pink and in grasses The stem may be more or less **hairy** It may be **prickly** or **spiny** If there are no hairs, and the stem is quite smooth, it is described as **glabrous** if, in addition, it is more or less shiny, with a bluish colour, it is said to be **glaucous** Hollow stems are described as **fistular**

§ 4 **Buds** (Fig 46) —The growth in length of the main stem or a branch takes place towards the apex At the extreme apex the internodes have not yet elongated the young leaves which are just in the course of development are crowded together and closely overlap the growing apex

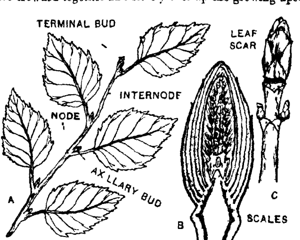


Fig 46 A Twig with Leaves and Buds B Winter Bud in Longitudinal [illegible]

of the stem or branch This compact structure, which we nearly always find at the apex of a stem, is called a **terminal** bud As growth takes place the internodes gradually elongate and the leaves become separated

It is important to notice that the branches of a stem make their first appearance as buds These buds which with reference to the stem on which they are borne are called **lateral** buds, are situated in the **axils** of the leaves, i e in the angle between the leaf and the upper part of

the stem The *axillary* position of the buds should be carefully noticed In the Angiosperms it is the rule that each leaf has a bud in its axil.

Very frequently, either naturally or owing to the influence of external conditions, only some of these buds develop into branches, the others remain quiescent In circumstances of necessity, however, as, for example, when the main stem and chief branches have been destroyed, these **dormant** buds become active, and give rise to *deferred shoots* Sometimes the shoots developed late on the stems of trees have this character

A bud, then, as found in the Flowering Plant, may be defined as a rudimentary or embryonic shoot, consisting of a short axis in which the internodes have not yet elongated and in which the young leaves are closely crowded together and overlap the apex. These buds can be recognised on plants at all seasons, but are most noticeable and are seen in the greatest variety, in winter

In many buds the young leaves are all of the same kind and in course of time develop into green foliage leaves but in most winter buds only the central leaves of the bud are of this kind, while the outer ones are small and scaly—*scale leaves*—and serve as a protection against cold and loss of water (Fig 46, B) In those regions of the Tropics where there is a regular alternation of dry and wet seasons many buds are similarly protected by bud-scales during the dry period In many winter buds the loss of moisture, which would be injurious to them, is more effectually prevented by the corky nature of the scales, by the secretion of mucilaginous or resinous substances (e g *Aesculus indicus*), or by the development of a covering of hair, as in the Jujube-tree (*Zizyphus*)

When the buds unfold in the rains the scales fall off and leave a zone or girdle of close-set scars The age of any particular part of a branch can be determined by counting the number of these zones between it and the apex of the branch They are well seen in the Pipul (***Ficus religiosa***), Silk cotton or Kapok (***Eriodendron***), etc

The **normal** axillary buds are developed in **acropetal** order (p 12) Buds which are developed out of their

proper order, or without any relation to the leaves, are called **adventitious.** The shoots of pollards and those developed on the trunks of many trees (*e g.* the Jak) arise from such buds. They may also be developed on leaves or roots If the leaf of the Begonia, for example, be artificially wounded and laid on the surface of the soil, adventitious buds are developed from the wounded surface and produce new plants. Buds occasionally arise naturally on the leaves of the succulent *Bryophyllum calycinum.* Adventitious buds commonly spring from the root in Dandelion, Rose, *Acacia dealbata* (Silver Wattle), and Coffee.

Sometimes more buds than one are developed in the axil of a leaf. These are called **accessory** buds. Examples are found in the Fuchsia, Barberry, *Capparis,* and Aristolochia.

§ 5 **Branching of the Stem.**—The branching of the stem in the Angiosperm is probably always **lateral** (p. 11), in other words, the branches arise as lateral buds in the axils of the leaves. The young leaves and their axillary buds originate as little protuberant outgrowths just below the extreme tip of the parent-axis. The branching may be **racemose** or **cymose** (p 12).

In indefinite or racemose branching (Fig. 3, B) there may be, at each node, either a single branch or a series (called a **whorl**) of two or more branches, according to the number of buds developed (which will depend largely on the number of leaves) Definite or cymose branching, if only one daughter-axis is given off at each branching, is said to be **uniparous** (Fig 47, A–D); if two, **biparous** (Fig 47, E), if more than two, **multiparous.** The biparous cymose form of branching, owing to the abortion of the growing-point of the parent-axis, frequently resembles a dichotomy, hence the name *false dichotomy* often applied to it. Examples are seen in the Cacti and Mistletoe.

In uniparous cymose forms the successive daughter-axes may be developed right and left alternately—the **scorpioid** form (Fig 47, A); or always on the same side—the **helicoid** form (Fig. 47, C). In these two forms the branching would present a zigzag or spirally coiled appearance

respectively, if the branches retained the position in which they are developed. But in nature the branching becomes straightened out (Fig. 47, B, D), and the basal portions of

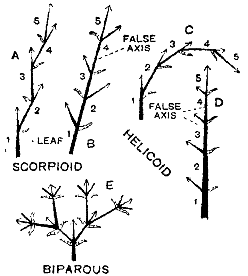


FIG. 47.—FORMS OF CYMOSE BRANCHING.
A—D, Uniparous

the successive daughter-axes constitute what *to all appearance* is a simple parent-axis, but is *really* a compound axis or **sympodium.** The scorpioid form resembles a typical raceme, the helicoid form a one-sided raceme. These *sympodial* forms are distinguished from true racemose ones by the position of the leaves, which, it should be noticed, are given off on the opposite side from what are *apparently* lateral branches.

The student is advised not to be content with a theoretical knowledge, but to make a careful practical study of branching by examination of a large series of plants. The racemose form is by far the commoner in purely vegetative

parts of stems; but cymose branching is frequently met with in trees—*e.g.* the uniparous form in the Vine and many rhizomes, where, owing to the death of the terminal bud at the end of the year, the growth in the following year is continued by a lateral bud. Types of branching are most easily recognised in herbaceous plants; in many woody plants (shrubs and trees), owing to the frequent loss or injury to which they are exposed, branching cannot be studied in its primitive condition, and the premature attempt to diagnose the more complicated forms of branching will inevitably lead to confusion.

§ 6. **Forms of Stems.**—We have already indicated that the various parts of plants are *adapted* to the performance of certain functions. The ordinary functions of a stem are (*a*) to bear the leaves and keep them expanded or exposed in such a way that they may best carry on their functions, (*b*) to serve as a conducting channel for various nutritive solutions passing between roots and leaves. These functions may, however, be carried on in many different ways, according to the mode of life of a plant, or peculiarities in its environment. Stems in different plants must have a structure and organisation adapted to the conditions in which they live. In addition to this stems may take on special functions. Thus they may serve as organs of vegetative propagation, or as storeplaces of nourishment, they may be specialised to act as protective organs, or to perform the functions usually carried on by other members.

The student will understand, then, that stem-structures assume an immense variety of forms, according to their special adaptations. Some (*e.g.* Foxglove, Sunflower, Lily) grow straight up, and are self-supporting, they are said to be "**erect.**" This is the typical form of stem. Others are **weak stems,** incapable of themselves of growing erect. Most stems are aerial, but many are buried in the soil, and are called underground or subterranean stems. Some are herbaceous; others are woody. Most woody plants form shrubs or trees, and are perennial, *i.e.* persist for a number of years. Herbaceous plants may be **annuals,** living only during one season, and dying down in the autumn; others

are **biennial** (*e g.* the Turnip), living during two seasons. In the first year they produce only vegetative shoots; in the second, flowers, fruits, and seeds. Many herbaceous plants, however, which die down in the autumn, perennate by means of their underground stems.

Some small shoots or twigs have only a limited development, and are called **"dwarf-shoots"**—for example, in the Jak, in which they are the twigs producing the flowers. Finally, in some plants, the stem is extremely short ("*reduced stems*") and the leaves *appear* to come off from the top of the root. Good examples are seen in the Radish and Carrot. We will now consider some of the more important of these forms.

§ 7. **Weak Stems.**—In some plants the stems are more or less prostrate or trail along the ground. Many weak stems, however, which are unable to grow erect themselves, make their way upwards by attaching themselves to surrounding objects. These are known as **climbing** and **twining** plants.

Many plants climb by *tendrils*, long thread-like organs with rapid growth and marked nutation (p. 193); these may be morphologically stems, as in *Vitis*, *Passiflora*, *Antigonon*, leaves (or parts of leaves) in many Leguminosæ, *Smilax*, etc., roots, as in *Vanilla*. In many tropical plants, e.g. *Artabotrys*, *Uvaria*, *Unona*, *Ancistrocladus*, *Strychnos*, the tendril is replaced by a sensitive hook—a modified inflorescence-axis—which thickens after catching and becomes woody. In *Gloriosa* the leaf-tip is sensitive and acts like a tendril. Others climb by hooks which are not sensitive, e.g. *Calamus* (Rattan), *Desmoncus*, etc., yet others by adventitious roots developed along the stem, *e.g.* many Aroideæ, *Ficus spp.* Pepper, and many ferns.

As distinguished from these, **twining plants** achieve the same result by themselves twining round some support, as, for example, *Ipomæa*, *Thunbergia*, *Mikania*, and others. The object in all cases of climbing or twining is, of course, to enable the plant to reach the light, which is necessary for the development of chlorophyll and for the assimilation of carbon dioxide (p. 13).

§ 8. **Runner, Offset, and Sucker.**—Many plants give off highly specialised shoots, serving chiefly for purposes of vegetative production Of these the runner, offset, and sucker are the commonest.

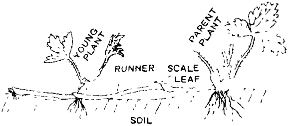


Fig 48 —Runner of Strawberry

The **runner**, or *stolon* (Fig. 48), is a very slender shoot running along the surface of the ground, and attaining a considerable length. It arises in the axil of a leaf, at the level of the soil At intervals it produces small scale-leaves, with a bud in the axil of each From the bases of these buds adventitious roots pass down into the soil, and in this way new plants are formed The Strawberry and the Hydrocotyle give good examples



Fig 49 —Offset

The **offset** (*e.g.* in *Furcræa* or *Pistia*) resembles the runner in origin, but is shorter and stouter. It is merely a short runner which turns up at the end to form a new plant

The **sucker** (Fig 50) is merely an *underground* runner or branch; it grows upwards, develops roots and aerial shoots These suckers are white or pink in colour, and resemble roots They are distinguished as stems, however, by their axillary development and the possession of scale-leaves. Good examples are seen in the Mint, Dead-nettle and Rose.

§ 9. **Bulbils.**—These may be described as axillary buds, which become large and fleshy owing to the storage of food-material in their leaves. They differ also from ordinary buds in the fact that they separate from the parent plant, fall to the ground, and produce new plants, thus serving for reproduction (*e g.* some Lilies). They may also take the place of flowers (*e g* in the Onion, *Agave*, *Furcræa*, some grasses, etc.) In plants producing them seed-formation is usually uncertain

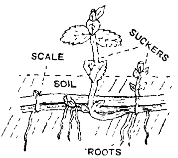


Fig 50 —Suckers of Mint.

§ 10 Underground Stems.

—The possession of underground stems enables plants to tide over periods unsuitable for aerial growth. They are thus a means of perennation and serve also for vegetative reproduction. There are several forms which deserve special mention.

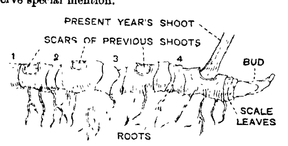


Fig 51 —Rhizome (Sympodial)
The numbers indicate the segments of the sympodium

The **Rhizome** is a stout elongated underground stem more or less filled with food-material (Fig. 51). Students are very apt to mistake the rhizome for a root. It is distinguished by the presence of leaves and buds (and also

by internal structure) The leaves may be large foliage leaves, but more frequently the rhizome bears only small brown scale-leaves, the foliage leaves being borne on the aerial shoots developed on the rhizome.

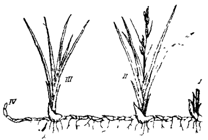


Fig 52.—Rhizome of Sedge (Carex) in Summer. Flowering shoots of (I) last year, (II) this year, (III) next year, (IV) year next but one.

Occasionally rhizomes are short and stand almost vertical, or run more or less obliquely through the soil, as in many Ferns In this case the misleading term *root-stock* has been given to them But usually the rhizome is a horizontal and dorsiventral structure.

Adventitious roots are given off from the surface of the rhizome It usually branches freely, and if these branches become separated they form distinct plants The aerial branches may be given off after the racemose type of branching, in which case the rhizome is monopodial in development (see p 12) and has a persistent apex (*e g* the Bracken Fern) In other cases the apex of the rhizome grows up into an aerial shoot, and the growth of the rhizome is continued by a lateral bud developed in the axil of a scale-leaf Here the rhizome is sympodial in development, being made up of the persistent basal portions of the successive growths, as indicated in Fig 51. Examples of sympodial rhizomes are found in the Plantain (*Musa*), Ginger, and *Canna*, and also in various

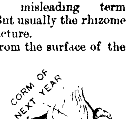


Fig 53.—Corm of Crocus. (Longitudinal section)

Reeds, Sedges, and creeping Grasses (Fig 52). As a rule, the scars of leaves and branches can be readily detected on a rhizome.

The Corm (Figs. 53, 54) is an underground shoot which may be regarded as a condensed form of rhizome. It consists of a massive swollen stem called the **disc,** on which are a number of loose, more or less sheathing scale-leaves The size of the disc is due to the large amount of food-material stored in it. One or more buds are present in the axils of the leaves, sometimes towards the apex of the disc (*e g.* in *Colocasia*, Fig. 54), sometimes towards the base (*e g* in *Colchicum*)

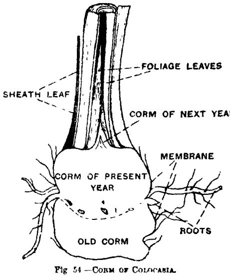


Fig 54 —Corm of Colocasia. (Longitudinal section)

In the spring these buds develop at the expense of the stored food-material, and grow up into aerial flowering shoots Adventitious roots are developed from the base of the bud, and pass down into the soil. During the summer the surplus amount of plastic substance is stored up in the basal portion of the new stem, and thus a new corm is gradually formed, which will in the same way produce new plants the following year.

Thus the corm represents the basal underground part of a stem, laden with food-material, and bearing buds and scale-leaves. Corms are *popularly* spoken of as **bulbs.**

The **Bulb** (Fig. 55) may also be regarded as a short specialised underground shoot. It has a structure somewhat similar to the corm, but the stem or disc is comparatively small, and the food-material is stored up in the large, fleshy scales which invest and overlap the disc These scales may either be scale-leaves, or the fleshy bases of foliage leaves whose upper parts have withered. A bud is present in the axil of one of the innermost scales and in the spring develops at the expense of the stored food-material into a flowering axis surrounded by foliage leaves, and also, it may be, by a number of scale-leaves Adventitious roots are given off from the base of the bulb

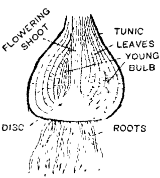


Fig 55 —TUNICATED BULB (Longitudinal section)

After flowering the food-material which is formed is stored up in the scale-leaves or in the bases of the foliage leaves, and in this way a new bulb is produced, which will repeat the process the following year Instead of a single bud, two or more may be present in the axils of the inner leaves In this case the new bulbs formed from them separate from the parent bulb

In **scaly bulbs** (*e g* Lilies, Tulips, etc) the fleshy scales, of which the main bulk of the bulb is composed, simply overlap at their margins In **tunicated bulbs** (*e g* Onion and Hyacinth) the outer leaves are large and completely ensheath the inner portions of the bulb The coloured membranous covering or tunic present on the outside of such bulbs is formed by the shrivelled remains of the leaves of a previous season.

Bulbs and corms are characteristic of plants which are exposed to the dangers of drought or of cold. They are found most commonly in monocotyledonous plants, but occasionally also in Dicotyledons.

The **Stem-tuber** (Fig. 56) is a swollen underground stem, or part of a stem, laden with food-material, and serving for purposes of vegetative reproduction, *e.g.* as the Potato and Jerusalem Artichoke

In the Potato the tubers are borne on slender underground shoots, which are recognised as such, not only by their internal structure, but also by the fact that they bear scale-leaves. The tubers make their appearance either at the apex of a shoot, or in the axils of the scale-leaves, and, instead of developing into normal branches, become enormously dilated by the deposition of starchy food-material The tuber, however, is readily distinguished as a modified stem-structure, not only by its position of development, but also by the possession of buds, known as the "*eyes*." When a tuber, or part of a tuber, is placed in the soil under proper conditions, the buds or "eyes" develop at the expense of the stored food-material, and produce new plants.

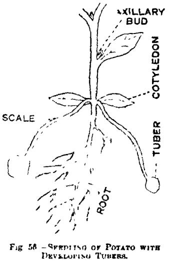


Fig 56 – Seedling of Potato with Developing Tubers.

§ 11 **Stem-Tendrils, Spines, and Cladodes.**—These are striking examples of more pronounced modifications of stem-structure which have arisen in adaptation to special conditions They are quite unlike ordinary stems, and assume forms which are also met with in morphologically different (dissimilar) members.

Stem-tendrils are highly specialised climbing organs. They are very slender, usually branch, may bear small scaly leaves, and are sensitive to contact. When in their growth they touch a suitable support, they twine under

it and the part of the tendril between the plant and the support becomes spirally coiled so as to raise up the part on which they are developed. Their morphological value is recognised by their position. Sometimes they represent lateral shoots In this case they arise distinctly in the axils of leaves, e g in the Passion Flower and *Antigonon* Others represent the modified apices of the successive shoots of a cymose branching (Vine and species of *Cissus*) In this case they do not appear in the axils of leaves, but are placed on the opposite side of the sympodial axis from the leaves (Fig 57, and cf. Fig 47, B, D)

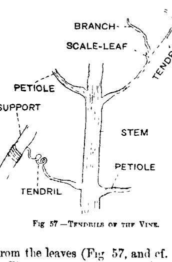


Fig 57.—TENDRILS OF THE VINE.

Stem-spines, or **thorns** (Fig 58), are modified branches which have lost their apical growing point and become hard and sharp-pointed Examples are seen in the Sloe, Hawthorn, and Gorse * The conversion of branches into thorns, by reducing the leaf-surface, diminishes transpiration, and, in this connection, it has to be noticed that they are commonly found on plants which live in dry situations. They also function, however, as protective organs Their stem-nature is recognised as before by their structure, by their position in the axils of leaves, and also by the fact that, though the terminal bud has



Fig 58.—SPINE OF THE SLOE

* And in *Alhagi maurorum*, an interesting plant of the Egyptian, Arabian and North Indian desert region.

been lost, they may bear lateral buds It is interesting also to notice that in the Plum, which may be regarded as the cultivated form of the Sloe, these structures are represented by leafy, flowering shoots.

The student must carefully distinguish between spines and prickles. The latter are irregularly developed, *i.e.* have no definite relation to the leaves, have no vascular tissue, and are very readily broken off.

A **cladode** or **phylloclade** is a stem-structure which has taken on the general appearance and functions of a leaf. The whole stem may be so modified. This is the case, for example, in the Duckweed, a small aquatic Monocotyledon in which the minute leaf-like stem acts as a float Usually, however, phylloclades represent lateral branches.

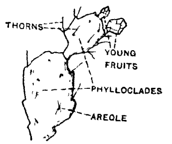


FIG 59.—PHYLLOCLADE OF OPUNTIA.

Phylloclades are mostly found in plants growing in dry or desert conditions, as, for example, in various plants belonging to the Cactaceæ and Euphorbiaceæ Under such conditions, in typical cases, the true leaves are either small or wanting, while the flattened leaf-like stems become more or less succulent, develop thick cuticles, and are adapted in other ways for storing up water and cutting down transpiration. The Opuntias, so common in India, have fleshy stems flattened like leaves; the true leaves are small and fleshy, and drop off very early.

Asparagus has green needle-like phylloclades.

§ 12. **The Torus or Thalamus.**—We have already mentioned (p. 8) that the flower is a specialised shoot. That part of the floral axis which bears the floral leaves (sepals, petals, etc) is called the *thalamus* or *torus*. It presents certain peculiarities, and must therefore be regarded as a special form of stem. It will be considered fully in the chapter on the flower.

§ 13. **Summary.**—We may summarise the general distinctive characters of the stem in the following statement stem-structures *tend* to grow *upwards, towards the light*; they usually end in a bud, and bear leaves, lateral buds, and often also reproductive organs, lateral branches (in Flowering Plants) arise in the axils of leaves; their development and internal structure are, in many ways, characteristic.

We cannot, however, regard this as of the nature of a definition, distinctly marking off stems from leaves and roots, for these general characters are not absolute. Thus we have seen that some stems (*e.g.* rhizomes) remain under ground and partake of the functions of roots, others have lost their terminal bud; in a few cases, again, buds are developed on roots and leaves. At the same time the student must notice these characters carefully, for it is by attention to these that he can as a rule recognise members which, however modified they may be, have the morphological value of stems. In this way, as already indicated, the rhizome, the sucker, the tubers of the Potato, and the spines of the Sloe, etc, can all be recognised as stem-structures

B INTERNAL STRUCTURE.

I *THE DICOTYLEDON.*

§ 14 **Primary Structure.**—The primary arrangement of tissue characteristic of the dicotyledonous stem may be studied in the Sunflower, *Carthamus*, or other herbaceous types. Fig 60 represents, diagrammatically, a portion of a transverse section of a well-developed internode of the Sunflower On the outside is the **epidermis** (p 56) The **fibro-vascular bundles** (p 62) are seen to be arranged in a ring Owing to this characteristic arrangement, the **ground-tissue** (p 62) is marked off into (*a*) a central region, the **medulla** or **pith**, (*b*) an outer region between the epidermis and the vascular ring, the **cortex**, and (*c*) a number of strands running between the bundles from pith to cortex, the **primary medullary rays.**

The pith, medullary rays, and inner region of the cortex consist chiefly of thin-walled *parenchyma* (p. 47). The hypodermal region of the cortex (the **hypodermis**), the region immediately under the epidermis, consists of *collenchyma* (p 48). In the cortical parenchyma, sometimes

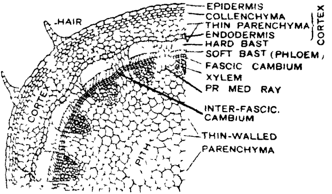


FIG 60 – PART OF A TRANSVERSE SECTION OF STEM OF SUNFLOWER.
The Inter-fascicular Cambium is not found in Young Internodes

also in the pith and medullary rays, small *resin-passages* can be detected, each with its *epithelial* layer (p 55) If the section be stained with iodine solution it is found that the cells of *the innermost cortical layer* contain starch-grains. This layer is then distinctly marked off from the rest of the cortex. It is the **endodermis** or **bundle-sheath.** Here, as in most stems, it is simply a *starch-layer*; its cells are not cutinised

Fig 61 represents the structure of one of the fibro-vascular bundles in transverse and also in longitudinal section. The bundles are **conjoint** (p 61). The **xylem** or *wood* is internal, the **phloem** or *soft bast* external; and there is between them a strip of meristematic tissue, the **fascicular** or **intra-fascicular cambium.** Bundles having the xylem and phloem placed side by side in this way are called **collateral.** When a cambium is present,

so that further growth (secondary growth) may take place, they are said to be **open.** The bundles of the Sunflower, then, are collateral and open.

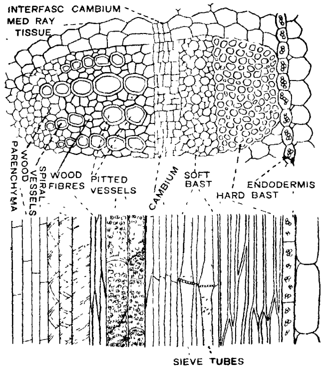


Fig 61 —Fibro vascular Bundle—Stem of Sunflower.
(Transverse and radial longitudinal sections)

The *primary* xylem contains annular, spiral, reticulate, and pitted vessels They are more or less arranged in radial rows, and amongst them is a tissue consisting of *wood-fibres* (p. 61) and *wood-parenchyma* (p 48). The smallest (annular and spiral) vessels are found in the

region of the primary xylem which lies next the pith. This is the region of the **protoxylem.** The phloem or *soft bast* consists of sieve-tubes, companion cells (p. 52), and phloem-parenchyma (p 61). The **companion cells** (Fig 28) are slender elongated cells, with dense proteid contents. The *hard bast* (p 61) and xylem, being lignified, are stained brown by iodine solution. The **cambium** is a single layer of thin-walled elongated cells which in transverse section are seen to be more or less four-sided and flattened. Towards the beginning of secondary growth, owing to the division of its cells, it seems to consist of several layers.

In some dicotyledonous stems no hard bast is developed, *e g* in the Wallflower. On the other hand, in many stems, instead of isolated bundles of hard bast, a complete ring of sclerenchymatous tissue is developed between the vascular bundles and the endodermis

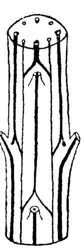


FIG 62 — DIAGRAM SHOWING GENERALLY THE LONGITUDINAL COURSE OF THE BUNDLES IN A DICOTYLEDONOUS STEM

§ 15 **Longitudinal Course of the Bundles.**—Fig 62 represents diagrammatically the longitudinal course of the bundles in a Dicotyledon Tracing one of these upwards, we find that it runs through one or two internodes, and then bends out into a leaf At the point where this bending takes place another bundle arises, runs upwards through one or two internodes, and passes out to a higher leaf. So with all the bundles of the ring. Or we might express it in another way, and say that bundles pass into the stem from the leaves, run downwards in the stem, and finally join on to bundles entering the stem from older leaves.

The bundles are **common bundles,** *i.e* they are not confined to the stem, but are common to stem and leaf. The upper part of the bundle, running obliquely through the cortex towards the leaf, is called the **leaf-trace.** In

the stem all the bundles run parallel to the epidermis, and at an equal distance from it. That is why, in transverse section, they form a ring. There is frequently considerable branching and intercommunication of the bundles at the nodes It follows that the primary medullary rays are of limited height.

In the stems of a few Dicotyledons *cauline bundles*, *i.e.* bundles confined to the stem, are found in addition to the usual common bundles. They usually run through the pith within the ring of common bundles and communicate with the latter at the nodes.

§ 16. **Distribution of Strengthening Tissue.**—It will be observed that the strengthening tissues in the Dicotyledon stem (xylem, sclerenchyma, collenchyma) are arranged near the periphery. It can easily be shown that this is the arrangement which best meets the strains to which the stem is subject A little reflection will show that the stem of a land-plant is mostly subject to bending strains (from wind and other influences) Now, if we bend a stem, it will be evident that the strain falls chiefly on the two sides of the stem. On the concave side the outer tissues will be compressed, while on the convex side they will be elongated. There is little or no strain in the middle. Thus the strengthening tissue will be most advantageously disposed near the periphery where the strain is greatest.

In roots, stems of water-plants, and other members, which must be able to bend and yet withstand pulling strains, the strengthening tissue, as we shall see later, is arranged in the centre. It may be taken as a general rule that the distribution of strengthening tissue in the various members of a plant is in accordance with the strains to which they are subject.

§ 17 **The Apical Meristem and Development of Tissues.**—Having now described the arrangement and the different regions of permanent tissue found in the fully grown herbaceous stem, let us see if we can trace any relation between these and the apical meristem from which they are derived. A longitudinal section (Figs. 63, 64) through the apical bud of a dicotyledonous stem shows

the apical meristem, and also the mode of origin of young leaves and branches. By examining such a section, and also a *regular* succession of transverse sections, we can trace the gradual differentiation of tissues

In some stems three regions can be distinguished in the apical meristem There is a single outermost layer passing right over the apex. If we trace this layer into the region of permanent tissue, we find that its cells divide only by walls at right angles to the surface; there are no divisions

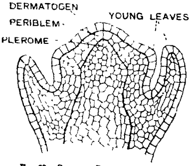


FIG 63 — GROWING POINT OF A STEM
(Longitudinal section)

parallel to the surface. Thus the layer remains single. It is the young or embryonic epidermis, and is called the **dermatogen.**

Internal to this is the second region, the **periblem.** At the extreme apex it may be a single layer; but behind the apex, owing to the irregular division of its cells, it becomes many-layered From it the cortical region of ground-tissue is developed. The periblem, therefore, is the young or embryonic cortex Its innermost layer becomes the endodermis, or bundle-sheath.

The third region forms the core, or central part of the apical meristem. It is known as the **plerome.** From this region is differentiated the whole of the central cylinder of tissue lying inside the endodermis, and including the vascular bundles, pith, and medullary rays.

The dermatogen is always very distinct; but it is only in a comparatively few stems—chiefly stems in which the apex is slender and the leaves are not numerous—that there is at the apex a clear distinction between periblem and plerome. In some stems the periblem and plerome seem to arise from a common group of initial (meristematic) cells, and become recognisable only at some distance behind the apex. Sometimes they cannot be distinguished at all;

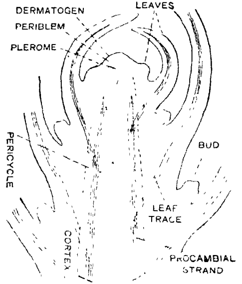


FIG. 61.—GROWING POINT OF A STEM.
(Longitudinal section—diagrammatic.)

and, occasionally, what appears to be the plerome is really the young pith, the tissue which gives rise to the bundles not being marked off from the periblem.

§ 18. **Development of the Vascular Bundles.**—At some distance behind the apex a number of longitudinal strands of elongated meristematic cells make their appearance near the periphery of the plerome. The divisions which take place in these cells are chiefly longitudinal, so

that, on transverse section, the cells appear smaller than the cells of the central region, which develops into the pith The strands are called **procambial** or **desmogen strands.** A transverse section (Fig. 65) shows that they are developed in a ring of similar small-celled tissue, forming the peripheral region of the plerome The strands develop into the vascular bundles; they are in fact the young or embryonic bundles.

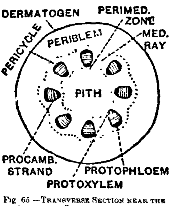


FIG 65 —TRANSVERSE SECTION NEAR THE APEX OF A STEM, ILLUSTRATING THE DIFFERENTIATION OF TISSUE.

(Diagrammatic)

In the differentiation of a procambial strand, the first xylem elements—the *protoxylem*, consisting of annular and spiral vessels—make their appearance on the inner side next the pith, the first phloem elements—*protophloem*—on the outer side Differentiation proceeds from these points towards the centre of the strand,* the later formed tissues being known respectively as *metaxylem* and *metaphloem* The differentiation, however, is incomplete A layer of meristematic cells persists in the middle, between the xylem and the phloem, as the *fascicular cambium*. This, being derived directly from the apical meristem, is a primary meristem (p. 46).

The longitudinal differentiation of the bundle shows considerable variety. In typical cases it begins at a node and extends from this point downwards into the internode and outwards into the leaf. The procambial tissue of *leaf trace* and leaf is developed in the periblem (see p. 151).

§ 19 **Conjunctive Tissue.**—The small-celled tissue around and between the procambial strands differentiates into ground-tissue, which being closely associated with the

* Thus with regard to the axis of the stem the differentiation of the xylem is *centrifugal*, that of the phloem *centripetal*.

vascular tissue is called **conjunctive tissue.** The vascular tissue and associated conjunctive tissue constitute what is called the **stelar system of tissue.**

The peripheral band of conjunctive tissue lying outside the ring of bundles and internal to the endodermis is called the **pericycle.** It may be a single layer of cells (*e.g.* Wallflower); but it usually consists of a number of layers. In the latter case it may consist entirely either of thin-walled tissue or of lignified tissue Most frequently, however, the portions of pericycle which lie just outside the bundles, and these only, are lignified, and form the ***hard bast*** of the bundles This lignification takes place later than the differentiation of the bundles Thus the hard bast, strictly speaking, does not belong to the bundle at all The intervening parenchymatous portions of the pericycle cannot be distinguished from the tissue of the medullary rays, which are developed from the tissue lying between the procambial strands.

The small-celled conjunctive tissue on the inner side of the bundles frequently forms a very distinct zone round the pith, called the perimedullary zone (Fig 65—it is not shown in Fig. 60). *In description it is not distinguished from the pith.*

§ 20. The relations which, in typical cases, exist between the regions of permanent tissue and the regions of apical meristem may be shown thus.—

Dermatogen →	Epidermis →			Epidermal System
Periblem →	Cortical Ground-tissue	Hypodermis General Cortex Endodermis		System of Ground-tissue
Plerome →	Pith →			System of Ground-tissue
	Stelar System	Conjunctive tissue	Pericycle Med rays Perimed zone	System of Ground-tissue
	Stelar System	Vascular Bundles →		Vascular System

§ 21 **Summary.**—The stems of most herbaceous Dicotyledons, and the young tender shoots of dicotyledonous shrubs and trees, have a structure agreeing in its general

characters with that just described. That is to say:—

(*a*) The apical meristem shows, more or less distinctly, dermatogen, periblem, and plerome.

(*b*) The bundles, in transverse section, form a ring, thus the ground-tissue is divided into regions known as cortex, pith, and medullary rays.

(*c*) The bundles are collateral, and most of them common. The xylem contains typical vessels, wood-fibres, and wood-parenchyma. The phloem contains sieve-tubes, companion cells, and phloem-parenchyma. Hard bast is often present as a lignified portion of a pericycle.

(*d*) The bundles are open, so that secondary growth may take place.

In many plants, belonging to the natural orders Cucurbitaceæ, Solanaceæ, Apocynaceæ, etc., each bundle contains one mass of xylem and *two* of phloem, one on the outside of the xylem and one on the inside The bundles are for this reason called *bicollateral*. Fig. 66 shows part of a transverse section of the stem of *Cucurbita* (Kaddu), which is a familiar instance of bicollateral bundles

§ 22. **Secondary Growth.**—We have now described the *primary* structure characteristic of dicotyledonous stems In herbaceous Dicotyledons it is *practically* the only structure to be recognised. On the other hand, in those perennial Dicotyledons whose aerial parts continue their growth from year to year, and which form shrubs and trees, this primary structure is completely modified by **secondary growth** which provides for the necessary extension of the vascular and other systems of tissue. By secondary growth is meant the formation of new tissue owing to the activity of a cambium layer, so that the member in which it occurs increases in thickness

The student must bear in mind that the cambium is a meristem. Its cells are capable of dividing and forming new cells, which are modified or differentiated into permanent tissue-elements. The new tissues thus formed are called *secondary* to distinguish them from the tissues differentiated from the apical meristem In considering

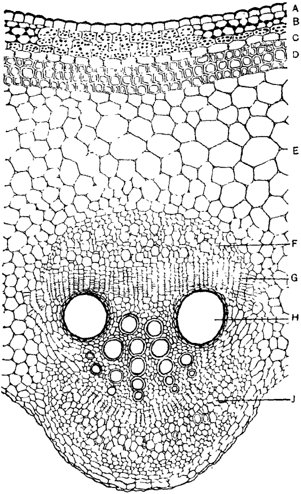


Fig 66.—Part of Transverse Section of *Cucurbita* Stem, showing a Bicollateral Bundle (*Inserted from "Practical Botany", with the kind permission of the author, Dr. F. Cavers*)

H, Xylem Vessel, F, Outer Phloem, J, Inner Phloem, G, Cambium.

this process we have to study the formation, not only of secondary vascular tissue, but also of secondary ground-tissue (phelloderm) and secondary tegumentary tissue (cork and bark).

§ 23. **Initiation of the Process.**—We have already seen that there is a layer of fascicular cambium between the primary xylem and phloem. When the process of secondary growth is about to begin, certain of the parenchymatous cells in each medullary ray also become meristematic. These strips of *secondary* meristem (p. 46) are called **interfascicular cambium** (Fig 60) They cross the medullary rays from one bundle to another, and join on to the fascicular cambium. In this way a complete ring of cambium—the **cambium ring**—is formed in the stem. This can readily be studied in the older internodes of *Helianthus*, where there are the beginnings of secondary growth, or in the young green twigs of trees.

§ 24 **Division of the Cambial Cells.**—The elongated cambium cells are tangentially flattened, and their end-walls are obliquely inclined (Fig 4, B) The method of division is as follows —Each cell divides *tangentially* (i e. by a wall at right angles to the radial direction) into an outer cell and an inner cell Of these one continues as a cell of the cambium The other may divide once or twice, but all the cells to which it gives rise are ultimately differentiated into permanent tissue The cell which continues as a cambial cell increases in size and again divides. As before only one of the two cells is differentiated. And so on.

§ 25. **The Secondary Tissue** (Fig 67).—The new cells formed by the cambium are given off on both sides—internal and external Those given off on the inner side are modified into wood elements—**secondary xylem**; those on the outer side, into phloem elements—**secondary phloem**.

It is evident, if the original position of the cambium ring be kept in mind, that the secondary xylem is laid down just outside the pith and primary xylem groups, and that, as a consequence of this, the cambium ring passes farther and farther from the centre of the stem, pushing in front of it the phloem-tissue both primary and secondary. In other words, the primary xylem and primary

phloem become widely separated from each other, owing to the intercalation between them of the tissue formed by, and on either side of, the cambium.

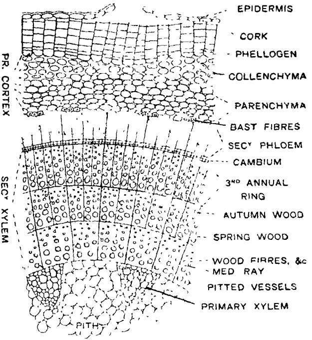


Fig 67.—Part of a Transverse Section of a three year-old Internode of a Dicotyledonous Stem. (Elder.)

The primary xylem bundles can still be recognised at the periphery of the pith, and form what is called the *medullary sheath*. The primary phloem lies on the outer side of the secondary. Pushed outwards as it is, and lying therefore on the circumference of a widening circle, it is subjected to lateral tension. For this reason it is very frequently spread out over the surface of the second-

ary phloem, and the original distinct groups of primary phloem are no longer recognised; but scattered groups of bast-fibres (representing the original hard bast, *i.e.* pericycle fibres) are frequently seen on the periphery of the secondary phloem.

Seeing that the interfascicular cambium as well as the fascicular produces this secondary tissue, there are no longer *wide* medullary rays running between pith and cortex. Certain cells of the cambium ring, however, instead of giving rise to wood and phloem elements, produce parenchymatous cells which form narrow medullary rays traversing radially the secondary wood and phloem. Strictly speaking, seeing that they are formed from the cambium, they consist of secondary tissue. Usually, however, those whose formation commenced at the beginning of secondary growth, and which therefore run (though they are very narrow) from pith to cortex, are still called primary, the term secondary being reserved for those whose formation began later, and which therefore start somewhere in the secondary wood and end somewhere in the secondary phloem.

The cambium ceases division during the winter. It renews its activity in the spring. Each year it forms a band of secondary wood and secondary phloem. The circular bands of secondary wood are distinctly marked off from each other, and are known as the **annual rings.**

The wood formed in the spring differs somewhat from that formed in the autumn. The former, the **spring wood,** consists of large, well-formed elements; the latter, the **autumn wood,** of smaller, more strongly thickened and lignified elements. This is partly owing to the greater activity of growth during the spring, partly because during the winter the pressure exerted by the outer tissues lessens slightly owing to the cracking of the cork. Occasionally more than one ring may be added during a year owing to fluctuation in the amount of food or water supplied to the cambium, but the number of annual rings indicates approximately the age of the stem.

This appearance is not seen in the phloem. Usually, as seen in transverse section, the phloem forms a continuous

circular band, traversed by narrow medullary rays. In some cases, however (e g. in the Lime), owing to the medullary rays expanding tangentially, by growth and division of their cells, the phloem seems to be made up of a number of conical masses with the apices directed outwards. The primary phloem groups are found at the apices of these.

The **secondary xylem** consists of wood-vessels, wood-fibres (sclerenchymatous fibres and tracheides), and wood-parenchyma. *It contains only pitted vessels* In rare cases there are no vessels; more frequently, e.g in Willows and Poplars, there are no tracheides. The function of the wood-parenchyma is to provide for the diffusion of nutritive products; it serves also for the storage of starch, and other products of metabolism. All the xylem elements being lignified give strength and rigidity to the stem

The **secondary phloem** frequently consists entirely of soft bast, but sometimes (e g in the Lime) it contains layers of bast fibres (hard bast) The soft bast contains sieve-tubes, companion cells, and phloem-parenchyma. The sieve-tubes and companion cells serve for the transport of proteid substance; the phloem-parenchyma for the transport and storage of carbohydrate substance.

The **medullary rays** are vertical plates of parenchyma traversing the wood and phloem in a radial direction Their cells are elongated radially. They are not usually more than one to a few cells wide In height they vary from two to about fifteen cells. They must not be thought of as sheets of tissue running continuously from the base of the stem to the apex. To understand properly the position of the medullary rays it is important to examine a tangential section of the stem. By means of the medullary rays the phloem and other tissues are supplied with water absorbed from the wood. On the other hand, through them the living cells of the wood receive nutritive substances which have been elaborated in the leaves and conveyed down the stem in the phloem.

§ 26. **Duramen and Alburnum.**—In old trees showing *many* annual rings, the central region of secondary wood becomes distinctly marked off from the peripheral region,

In the central region the wood-cells (wood-parenchyma) lose their contents, and the walls and cavities of the xylem elements are filled with tannin and other substances, which give a dark colour to the wood and preserve it from decay. This dark-coloured central region of the xylem is called the **duramen** or *heart-wood*; the peripheral region, which alone serves for the transference of watery solutions, is the **alburnum** or *sap-wood*.

§ 27. **Phellogen.—Formation of Cork** (Fig 67).—It is evident that this internal formation of secondary wood and phloem must exert considerable pressure on the peripheral tissues (cortex and epidermis). The epidermis is stretched and eventually ruptured. To provide for this there is the formation of new tissue from another cambial layer developed in this region. This cambial layer, which arises as a secondary meristem, is the **phellogen** or **cork-cambium.**

In the majority of cases (*e.g.* in the Elder) the phellogen has a superficial origin in the outermost layer of the cortex, immediately underneath the epidermis. At some stage in the process of secondary growth, the cells of this layer become meristematic. The young cells given off to the outer side of the phellogen are suberised, and form a tissue known as **cork** or **periderm** (see p. 50). This tissue being impermeable to water cuts off the epidermis from nourishment. The epidermis dies and gradually peels off as the first bark of the tree. The cork is the secondary tegumentary tissue developed to replace the epidermis and carry on its functions.

New cells may also be produced on the inner side of the phellogen. The tissue thus formed is parenchymatous and is added on to the primary cortex. It is the **phelloderm** or *secondary cortex*. This tissue, however, is frequently absent (Fig. 67), or only sparingly developed, during the first few years of secondary growth.

Although the phellogen of the stem *usually* originates in the outermost cortical layer, it may arise in other layers. Thus in Willows it originates in the epidermis itself. Sometimes it is the second or third layer of the cortex which becomes meristematic, *e.g.* in the Laburnum. In Clematis, the Vine, and others, the first phellogen arises in the pericycle. In these cases the first bark con-

sists not only of the dead epidermis, but also of all cortical tissue external to the phellogen. It may be taken as a general rule that the deeper the origin of the phellogen, the earlier and more abundant is the formation of phelloderm.

§ 28. **The Bark** may be defined as all dead tissue lying outside an active cork-cambium. We have already indicated what the first bark consists of The first phellogen formed may persist for a large number of years, *e g.* in the Birch; in the Beech it persists throughout the life of the tree. This is the case only where the first phellogen has a superficial origin. In such cases there may be a considerable formation of bark owing to the dying off of the older cork-layers.

But in most cases this first phellogen dies, sooner or later in those plants where it has a superficial origin, early in those where it is deep-seated It is replaced by a new or secondary phellogen developed in the deeper tissue This produces a new cork-layer, and as a result all the outlying tissues (the original cork, etc.) die and are added to the bark If the succession of secondary phellogens is rapid it often happens that the phellogen comes to lie close to the phloem In some cases, even, the new phellogens may arise in the phloem, *e.g* in the Vine and Clematis.

In some trees the bark comes away in sheets, and is spoken of as **ring-bark.** This may be due either to the fact that the first phellogen is persistent, *e g.* in the Birch (Bhojpatra), or to the fact that the successive phellogens appear in the form of regular rings But in many trees the bark is given off in scales —**scale-bark** — *e g* in the Plane. This is due to the fact that the secondary phellogens do not arise as regular rings or layers, but in the form of little tangential strips abutting on the previous phellogen.

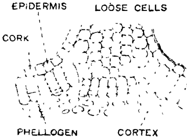


Fig 68 —Section through a Lenticel.

§ 29. **Lenticels** (Fig 68).—In the young green shoot, the epidermis, as we have seen, has stomata allowing for the interchange of gases and water-vapour. When the cork-tissue is developed we usually find certain structures known as **lenticels** having the same function. These form small oval scars on the brown surface of the shoot (*e.g.* in the Pipul). Sections show that at these points the cork-cells are not in close contact, but have separated from each other and form a loose, granular, or powdery mass through which gases and vapours can readily pass.

The lenticels are as a rule developed immediately underneath the stomata. Where a thick mass of cork is developed they form long passages or canals, filled with the powdery cork-cells, as, for example, in the ordinary cork of commerce. The lenticels are closed during winter by the formation of ordinary cork-tissue

II. *THE MONOCOTYLEDON.*

§ 30. **The Typical Arrangement.**—Fig. 69 shows the typical arrangement of tissues in the monocotyledonous stem, as seen in transverse section. There is a large number of vascular bundles *scattered irregularly* through the ground-tissue. They are smaller and closer together at the periphery of the stem than in the centre. Owing to this **scattered arrangement** of the bundles, the ground-tissue is not marked off into pith and medullary rays.

The ground-tissue consists chiefly of thin-walled parenchyma, but just under the epidermis there *may* be patches of collenchyma or sclerenchyma. In addition to this there is, in *many* monocotyledonous stems, a stout band of sclerenchyma, called the **strengthening zone**, developed just outside the region containing the bundles. This strengthening zone is the lignified sclerenchymatous **pericycle.** The layer of cells immediately outside it is the **endodermis,** which, however, is usually very faintly marked in Monocotyledons. The endodermis, as in Dicotyledons, is the innermost layer of the cortical ground-tissue. In the monocotyledonous stem the vascular tissue

of the stelar system separates into a number of distinct collateral bundles, each invested by its own sheath of lignified conjunctive tissue (sclerenchyma, Fig. 70).

While this arrangement is found in many monocotyledonous stems, e g in *Ruscus* (the Butcher's Broom) and in Asparagus, it should be carefully noticed that in others the pericycle and endodermis are not marked off by special characters from the rest of the parenchymatous ground-tissue—*e g.* in the Maize.

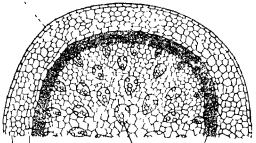


Fig 69.

HALF OF A TRANSVERSE SECTION OF A MONOCOTYLEDONOUS STEM. (Diagrammatic)

The tissue between the bundles is thin walled parenchymatous ground tissu

§ 31. **The Vascular Bundle** (Fig 70) —The bundles are **collateral** The xylem is directed towards the centre of the stem, and is usually more or less distinctly V-shaped Large pitted vessels, one or more, are situated on each arm of the V. The protoxylem vessels occupy the apex of the V. In some plants, *e.g.* in the Maize, an air passage is lysigenously formed by the breaking down of one or

more of the annular vessels. The phloem lies between the arms of, but, as a rule, slightly outside, the V. It consists of sieve-tubes with small companion cells; there is no phloem-parenchyma. On its outer side small protophloem

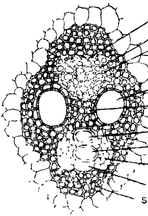


FIG. 70.—TRANSVERSE SECTION OF VASCULAR BUNDLE OF MAIZE.

elements can often be recognised, but there is **no hard bast.** The reason of this will be evident if the student remembers that the hard bast in the Dicotyledon is a lignified portion of the pericycle. The bundles are **closed,** i.e. there is no cambium, and therefore no secondary growth.

§ 32. **Longitudinal Course of the Bundles** (Fig. 71).—The bundles are *common.* The leaves have usually a broad insertion, and from them a number of bundles can be traced into the stem. Their downward course in the stem is not parallel to the surface, but curved. They first run obliquely downwards towards the centre, and then bend outwards again towards the surface. After running through one or two internodes they join on to bundles passing in from older leaves. At all levels then we ob-

viously have bundles situated at varying depths in the ground-tissue, and it is for this reason that the transverse section shows a scattered arrangement.

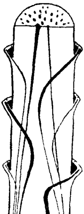


FIG 71 —LONGITUDINAL COURSE OF THE BUNDLES IN THE MONOCOTYLEDON. (Diagrammatic)

§ 33. **Apical Meristem and Differentiation of Tissues.**—In the apical meristem *dermatogen*, *periblem*, and *plerome* can be more or less clearly distinguished as in the Dicotyledon. The dermatogen gives rise to the epidermis, the periblem to the cortical ground-tissue, and the plerome to the tissues within this. As already indicated, the endodermis (innermost layer developed from the periblem) and hypodermal tissue (collenchymatous or sclerenchymatous) may or may not be distinctly marked off. The pericycle may or may not be sclerenchymatous Scattered procambial strands appear in the plerome Differentiation of vascular tissue takes place as in Dicotyledons, but is complete, so that no cambium is left

§ 34 **Modifications.**—Sometimes the bundles are not *irregularly* scattered, but confined to particular regions of the ground-tissue. In the Black Bryony (*Tamus communis*), for example, they run in the region of ground-tissue immediately inside the strengthening zone. In this case there is a superficial resemblance to the dicotyledonous arrangement In Grasses the central region of the ground-tissue in the internodes has been absorbed, so that the internodes are hollow, and the bundles run in the ground-tissue (derived from the plerome) near the epidermis. Finally, in a few Monocotyledons—Yucca, Dracæna, etc.—there is a form of secondary growth. It is only in these few forms that we meet with secondary growth among Monocotyledons

Certain examples of monocotyledonous *trees* may occur to the student, such as the Palms. In these, however, there is no secondary growth. The whole of the tissues of the stout palm-stem are derived from a *huge* apical meristem. In Palms there is the typical scattered arrangement, though the tissues undergo much thickening and lignification.

§ 35. **Exceptional Secondary Growth.**—In Yucca, Dracæna, and a few others, there is a form of secondary growth. In the primary condition of the stem there is the typical scattered arrangement of common bundles which are closed. A cambium originates *in the pericycle* entirely as a secondary meristem. It gives rise to new tissue on the inner side only, and this tissue is differentiated into new secondary bundles with intervening ground-tissue. The new bundles are *cauline* (p. 96). A phellogen (secondary meristem) also develops beneath the epidermis, and produces cork.

III GENERAL

§ 36 **Origin of Lateral Branches.**—In both Dicotyledons and Monocotyledons axillary buds have a superficial origin from the apical meristem of the parent-stem. They arise as little protuberances of dermatogen and periblem only (Fig 64) The plerome of the parent-axis takes no part in their formation For this reason their development is said to be **exogenous.** As the axillary protuberance increases in size a plerome (derived from the periblem of the parent axis) differentiates, and becomes connected with the plerome of the parent. Young leaves begin to grow out and overlap the apex Thus we have an axillary bud which in all respects reproduces the structure of the apical bud of the parent-axis

§ 37. **Healing of Wounds.**—When a stem (or other member of a plant) is injured, the outermost uninjured layer of living ground-tissue forms a meristem (phellogen), producing a cork-layer which protects the wounded surface. This power of healing wounds is possessed by Monocotyledons as well as by Dicotyledons.

Frequently, in woody plants, the uninjured cells adjacent to the wounded surface do not directly produce a cork-layer, but give rise to a succulent mass of parenchymatous tissue called the *callus* * This fills up and covers the

* This tissue is to be distinguished from the substance of the same name deposited on the sieve-plates in autumn (p. 52).

wound, and cork is formed on its surface. If the cambium is injured, the cells of the callus form a fresh strip of cambium, which becomes connected with the injured layer, and thus provision is made for the continued formation of secondary tissue.

When a branch of a tree is cut or broken off, a covering of callus is developed from the cambium layer round the margin of the exposed surface. The cambium developed in this produces secondary tissue, which, in course of time, completely buries the stump. This is the origin of the *knots* so frequently met with in the wood of trees. The hardness of the knot is due, of course, to the pressure of the surrounding wood. When plants are propagated by means of cuttings, there is a similar formation of callus on the cut surface.

CHAPTER V.

THE ROOT OF THE ANGIOSPERM.

§ 1. **General Characters.**—The root may be defined as that member of a plant which tends to turn downwards, away from light and towards water; which, as a rule, bears neither leaves nor buds, and which usually has at the apex a protective cap of tissue called the **root-cap.** The internal structure and development, also, are characteristic. It is by consideration of these characters that true roots can be distinguished from root-like stems.

A. External Characters

§ 2 **Tap and Adventitious Roots.**—As already explained, the terminal portion of the radicle is the embryonic or primary root. In the majority of *Dicotyledons* the primary root, at germination, elongates, grows down into the soil, branches, and forms the root-system of the plant This is known as a *tap-root system.* The elongated primary root is described as a **tap-root,** and the branches, if developed in regular acropetal succession, as *normal secondary roots.* The branching is invariably lateral. Where an *elongated* tap-root bears normal secondary roots the branching is *racemose* (Fig 56). Where the parent-root remains short, and the normal branches form the extensive root-system, the branching may be compared with the *cymose* type (Fig 72)

Instead of normal roots, however, we may find **adventitious roots.** These are roots developed (*a*) on other roots, but not in the normal order of acropetal succession; (*b*) on stems; (*c*) in a few cases on leaves. Adventitious roots

also are common in dicotyledonous plants, more especially in those with rhizomes, runners, trailing stems, etc. (*e g* Figs 50, 51). In *Monocotyledons*, in nearly all cases, the roots are adventitious (see p. 75)

§ 3. **Functions and Adaptations of Roots.**—Like stems, roots have a form and organisation adapted to their mode of life and the conditions in which they live Only where they are exposed to light do they contain chlorophyll, and help to a certain extent in carbon-assimilation. They are *usually* buried in the soil, and, for this reason, are not exposed to such a diversity of influences as stems. Their environment being less complex, they naturally show less variety in form and adaptation.

At the same time, the functions of an ordinary root—(*a*) the fixation of the plant, (*b*) the absorption of nutritive solutions from the soil—may be carried on in many different ways, according to the nature of the soil or the needs of the plant. We find also that roots may take on special functions They may, for example, function as storeplaces of nourishment, or as climbing organs Sometimes they are aerial, sometimes aquatic. In a few cases roots are more highly specialised as floats, spines, and so on. For these reasons the forms and adaptations of roots are by no means few

§ 4. **Forms of Tap- and Normal Branch-Roots.**—The most typical form, found more especially in herbaceous Dicotyledons, is the *fibrous branching tap-root* Here both the main or tap root and the normal branches are elongated and slender, more or less resembling fibres (Fig 56). Such roots are found only in "deep-feeding" plants A modification of this is the short stout primary root, with an extensive

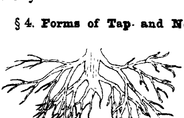


FIG 72 —SHORT PRIMARY ROOT WITH FIBROUS NORMAL BRANCHES.

system of fibrous normal branches (Fig. 72). Such roots are found in "surface feeders."

Annual roots are usually thin and fibrous and contain no stored food-substance. Perennial roots, on the other hand, have more or less reserve material providing for next year's growth, and may become thick and fleshy, as in the Sweet Potato. For the same reason the root in biennial plants may be greatly thickened, as in Carrot, Beet, Radish, and Turnip (Fig. 73). It should be noticed, however, that the so-called tap-root of the Carrot and Beet

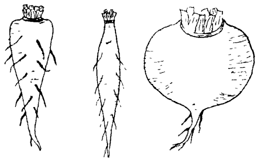


Fig 73 —FORMS OF THICKENED TAP ROOT.

(**conical tap-root**) really includes the hypocotyl, while in English Radish (**fusiform tap-root**) and Turnip (**napiform tap-root**) the swollen part consists entirely of the hypocotyl. Sometimes normal secondary roots become swollen and tuberous, forming *normal root-tubers.*

§ 5. **Forms of Adventitious Roots.**—Adventitious roots are usually slender and **fibrous**, as in Grasses But frequently, owing to storage of food-material, they become **tuberous,** as in Dahlia, Paeony, and many Orchids. These root-tubers may be simple and undivided; or double, *i.e.* branched into two (**double tuber**); or branched in a finger-like manner (**palmate tuber,** Fig. 74). In

Dahlia and Paeony the tuberous roots grow out from the base of the stem (Fig. 75). In Orchids they are developed adventitiously from buds produced at the base of the season's shoot. In the following year the buds develop into new aerial shoots at the expense of the material stored up in the tubers.

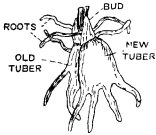


Fig 74 —PALMATE TUBER OF AN ORCHID

Sometimes adventitious roots are *aerial*, as in many Orchids, where they are adapted for absorbing moisture from the air Occasionally aerial roots function as climbing organs (*root-tendrils*), e g in the Ivy Many plants have what are called **parasitic roots.*** These plants, instead of deriving their food-material in the usual way, send "suckers" (*haustoria*) into other plants and absorb their nutritive juices

§ 6. **The Root-Hairs** (p 60) are developed on roots a short distance behind the root-cap. They do not persist behind this region. Besides acting as absorbing organs they play an important part in the fixation of the plant, as the particles of soil firmly adhere to them. They are well seen on the roots of seedlings grown in moist sand (Fig. 76).

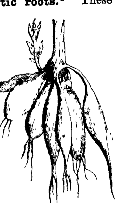


Fig 75 —TUBEROUS ROOTS OF DAHLIA

* According to some these are not true roots, but structures of the nature of emergences (p 60) They differ from simpler emergences in having a core of vascular tissue, and from most roots in being usually exogenous in origin

B. Internal Structure

§ 7. **The Apical Region.**—Fig. 77 represents diagrammatically a *median* longitudinal section of the radicle of the embryo of the Almond or Sunflower. See also Fig. 78. Covering the apex is the root-cap, which, as has already been indicated (p. 56), is a many-layered epidermis. Beneath this is the meristem, which gradually passes farther back into the older tissue of the root. The meristem

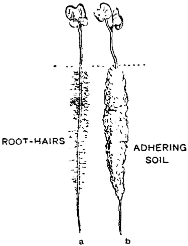


Fig 76.—Mustard Seedlings.

shows, sometimes very distinctly, the same regions as in the stem—**dermatogen, periblem, and plerome.***

The dermatogen cells *usually* divide by both perpendicular and tangential walls, so that at the apex of the root

* This differentiation into three primary layers, whether in stem or root, must not however be regarded as by any means universal in plants.

it forms the many-layered root-cap. The periblem, as in the stem, gives rise to the cortical ground-tissue. The plerome gives rise to the central cylinder containing the vascular tissue with its associated conjunctive tissue. **Procambial strands** make their appearance in it, and, on further development, these are *completely* differentiated into vascular bundles—some into xylem bundles, others

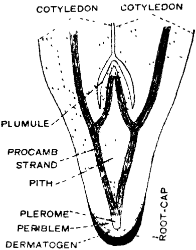


Fig 77.—Longitudinal Section of Embryo of Sunflower (Lower Part only)
(Diagrammatic)

into phloem bundles The differentiation of both xylem and phloem bundles begins on the outer side of the procambial strands, *i.e.* the development is centripetal.

In most Dicotyledons the root-cap tissue shades off farther back into a single layer, which produces the root-hairs In most monocotyledonous roots, as can readily be recognised in a similar section of the radicle of the Maize, the same structures are seen; but here the tissue of the root-cap peels off completely, so that behind the apex the

superficial layer is the outermost layer derived from the periblem (Fig. 78). The layer of meristem from which the root-cap is formed is sometimes called the *calyptrogen*

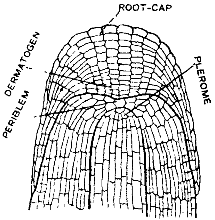


Fig 78 —Longitudinal Section through the Tip of the Radicle of a Monocotyledonous Embryo.

§ 8. **Primary Structure of Roots.**—A transverse section of a monocotyledonous or of a young dicotyledonous, root (Figs. 79, 80) shows a varying number of vascular strands, or bundles, more or less aggregated towards the centre. These bundles, developed from procambial strands, are not conjoint, but consist of phloem only, or xylem only. The **xylem** and **phloem bundles** are equal in number, and alternate with each other, so that they are situated on different radii of the transverse section They are separated by *conjunctive tissue*. It is important to notice that the stele is *exarch*, i.e. the protoxylem elements (annular and spiral) lie towards the periphery, and not, as in the stem-bundles, towards the centre (*endarch*).

In many roots all the xylem bundles fuse or meet in the

centre of the root in a number of large pitted vessels; in this case there is no pith. In others, the centre of the root is occupied by a parenchymatous, sometimes sclerenchymatous, tissue, which may simply be called the **pith**.

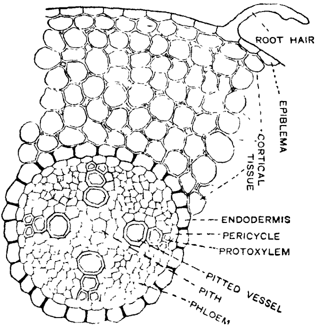


Fig. 79.—Transverse Section of a Young Dicotyledonous Root with Tetrarch Stele.

The vascular cylinder is surrounded by two special layers of cells. The inner layer consists of parenchymatous cells with protoplasmic contents, and is the **pericycle.** It is the outermost layer of conjunctive tissue (cf. the stem). In the roots of Angiosperms it is usually a single layer. The outer of the two layers is the **endodermis** or *bundle-sheath,* and is the innermost layer

of cortical tissue developed from the periblem (cf. stem). Its cells in transverse section are four-sided, and slightly elongated tangentially.

In the typical endodermis the radial walls of the cells are cutinised and have a wavy, uneven character, so that, as seen under the microscope, they appear less definite and somewhat darker than the others (Fig 79). There are no spaces between the endodermal cells. While, therefore, the endodermis permits the diffusion of liquids it forms an airtight membrane, which prevents the passage of air from the cortical tissue to the central cylinder. Behind the absorbing region of the root the walls of the endodermal cells, more especially the radial and inner walls, are often strongly thickened and cutinised (Fig. 80).

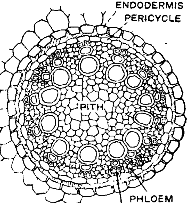


Fig 80 —Transverse Section of the Central Part of the Root of Iris, showing the Polyarch Stele.

Outside the endodermis lies the parenchymatous cortical tissue. The outermost layer of the root is called the **piliferous layer,** or **epiblema.** These terms are used instead of epidermis, because, as we have seen, this outermost layer has not a constant morphological value,—sometimes being a true epidermis (Dicotyledons generally), sometimes the specialised outermost layer of the cortical tissue (Monocotyledons generally). Sometimes the layer internal to the epiblema consists of large cells, or is otherwise distinguished; it is called the *exodermis*.

§ 9 The vascular cylinder in roots was formerly regarded as a compound vascular bundle, and described as a *radial vascular bundle*, because the xylem forms a number of rays with alternating

groups or patches of phloem. It was placed on a level with, and compared with, the collateral bundle of the stem. This radial arrangement of vascular tissue is characteristic of roots, but we have now to recognise that the vascular cylinder of the root is a stele, containing a number of bundles (in addition to conjunctive tissue), and is, therefore, comparable, not to a single collateral bundle, but to the whole stelar system of the stem. This type of stele has been termed an **actinostele**.

In the alternating positions of the xylem and phloem strands, and in the exarch character of the protoxylem, the structure of the root is remarkably uniform, not only in the Angiosperms, but in all Vascular Plants.

10 Monocotyledonous and Dicotyledonous Roots. —While in monocotyledonous and *young* dicotyledonous roots the *general arrangement*, as already described, is the same, there are several very characteristic points of difference in detail:—

(*a*) In *Dicotyledons* (Figs. 79, 81, 82) the number of xylem bundles *usually* varies from two to five, although there may be more than five.

In *Monocotyledons*, while a limited number—about five to eight—is sometimes found (*e.g.* root of Leek), there are usually many more than this—as many as twelve to twenty (*e g.* roots of Iris or Maize, Fig. 80). Where there are only two xylem (and two phloem) bundles, the stele is described as *diarch*; where three, *triarch*, four, *tetrarch*; five, *pentarch*; many, *polyarch*.

(*b*) In both Dicotyledons and Monocotyledons the differentiation of procambial tissue is *complete*; but, in most Dicotyledons, a cambium, and later a phellogen, arise as secondary meristems, and secondary growth takes place; in these the structure above described is only the *primary* structure.

In Monocotyledons, on the other hand, there is no secondary growth in the thickness, and the same structure can be recognised in all the fully developed regions of the root.

(*c*) In Monocotyledons the pitted vessels are large and nearly circular in transverse section; in Dicotyledons they are usually much smaller, and more or less polygonal.

§ 11. Secondary Growth in the Dicotyledon (Figs. 81-83).—When secondary growth is about to begin, certain conjunctive cells lying on the inner side of each phloem bundle become meristematic (Figs. 81, 82). Thus strips of **cambium,** equal in number to the phloem bundles, make their appearance. These gradually extend outwards between the xylem and phloem bundles, *owing to more of the conjunctive parenchymatous cells becoming meristematic.*

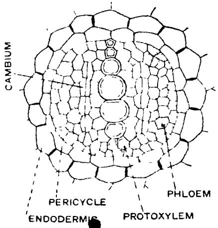


FIG 81.—TRANSVERSE SECTION OF THE DIARCH STELE OF A DICOTYLEDONOUS ROOT.
The origin of the Cambium is shown.

The curved strips of cambium thus produced come into contact with the pericycle on each side of the protoxylem. These pericycle-cells now become meristematic, and, in this way, the cambium strips are united and become continuous round the tips of the protoxylem groups. Thus a continuous wavy band of cambium is formed, running internal to the phloem bundles external to the xylem. It should be recognised that this cambium is entirely a secondary meristem, arising partly from parenchymatous cells between xylem and phloem, partly from the pericycle

The cambium-cells divide exactly as in the stem. The **secondary xylem** (Fig. 83) is laid down around the pith (if present) and the primary xylem bundles. The **secondary phloem** is formed outside the cambium, and, together with the primary phloem and other tissues, is gradually thrust outwards as the cambium adds to the secondary xylem The cambium-cells on the inner side of each primary phloem bundle are the most active, and, owing

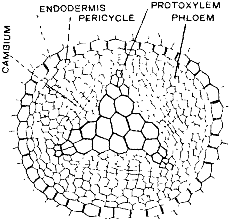


FIG 82.—TRANSVERSE SECTION OF TRIARCH STELE OF ROOT OF ELDER. (Secondary growth is beginning.)

to this, the cambium-layer as a whole, which was at first a wavy band (in transverse section), soon becomes circular.

The cambium-cells lying just outside the primary xylem bundles, instead of giving rise to secondary wood and phloem, usually produce strands of parenchyma—the *main* (also called primary) *medullary rays*—radiating outwards through the secondary wood and phloem from the tips of the protoxylem groups. If a very compact secondary wood is formed, it may be difficult to detect the primary xylem bundles, or the main medullary rays Small secondary medullary rays also are formed from the cambium-cells.

If the primary structure and the subsequent development be borne in mind, it is evident that the primary phloem bundles should be found just outside the secondary phloem on radii alternating with the primary xylem bundles, but, frequently, as in the stem, they are more or less disorganised and mixed with the secondary phloem.

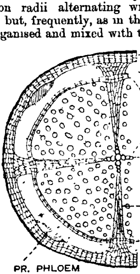


Fig 88 —Transverse Section of Dicotyledonous Root after Secondary Growth.
(Diagrammatic.)

If there is any considerable secondary growth, the pericycle, sooner or later, becomes completely meristematic, and forms a **phellogen**, or *cork-cambium* (a secondary meristem). This phellogen produces cork externally, and usually also, internally, a considerable amount of phelloderm (as in most deep-seated phellogens) Lenticels may be developed. The endodermis and cortical tissue die, and are given off as *bark*. It is comparatively rarely in roots that the phellogen has a superficial origin.

§ 12. **Anomalous Secondary Growth.**—In the roots of a few Dicotyledons the first cambium ring after a time becomes inactive, and a new cambium arises in the pericycle or in the phelloderm. This in its turn, after producing a ring of xylem and phloem, is

similarly replaced. In this way a series of concentric rings, consisting of secondary xylem and phloem, is formed in the root. This can easily be observed in the root of the Beet

§ 13. **Development of Lateral Rootlets** (Fig. 84) — Normal root-branches are usually developed, in Angiosperms, entirely from the pericycle. The cortical tissue of the parent-root takes no part in the formation of the tissues of the lateral branch This development from a deep-seated layer is called **endogenous.**

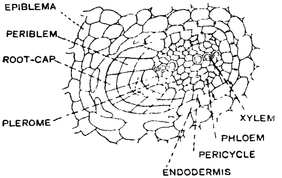


Fig 84 — Transverse Section of a Dicotyledonous Root (with Diarch Stele), showing the Development of a Lateral Rootlet

The development begins some little distance behind the apex of the parent-root, but before secondary growth has set in. The young lateral roots generally make their appearance in the pericycle just outside the protoxylem groups, so that the number of longitudinal rows of lateral roots usually corresponds to the number of xylem bundles in the stele. Thus, if there are four xylem bundles, there will usually be four longitudinal rows of normal lateral branches.

When development begins, the cells of the pericycle divide, *i.e.* become meristematic, and produce a growing-point, which soon shows a distinction into dermatogen, periblem, and plerome. The young branch-root gradually

elongates, boring its way through the overlying cortical tissue till it reaches the surface of the parent-root. At first the endodermis and, it may be, one or two layers of cortical cells form a sort of cap over the apex of the developing rootlet. This is known as the "*digestive sac*" because it secretes a ferment which disorganises or digests the walls of the overlying cells and so enables the young root to reach the surface. The structure of the lateral root is identical with that of the parent-root.

In Dicotyledons it is evident, considering the points at which the rootlets are developed, that after secondary growth has begun they will be seen (in a transverse section) radiating out from the tips of the primary xylem bundles, and therefore running as it were through the main medullary rays.

Adventitious Roots are developed similarly. If they are developed from the stem, they originate in the pericycle of the stem.

§ 14. **Exceptional Cases.**—Not uncommonly lateral rootlets are developed from the pericycle opposite the phloem bundles, *e g.* in many Grasses where the pericycle is wanting opposite the protoxylem, and in many Umbelliferæ where an oil-duct lies in the pericycle opposite each protoxylem group. Often when the stele is diarch there are four rows of lateral rootlets, two being developed opposite the phloem.

§ 15 **Secondary Growth in Monocotyledons.**—Exceptional secondary growth is found in the roots of a few monocotyledonous plants—Dracæna, Yucca, etc. The meristem-ring originates as a secondary meristem either in the pericycle or in the cortical tissue, or partly in one, partly in the other. There is also cork-formation, the phellogen originating in the superficial cortical tissue beneath the epiblema. There are a few other monocotyledonous plants in which a similar formation of cork occurs in the root, although there is no secondary formation of vascular tissue (*e.g.* in the Iris).

§ 16 **Functions of the Pericycle.**—The pericycle is an important layer in the root, and the functions discharged by it should be carefully noted. Its cells have a great capacity for remaining or becoming meristematic In both Monocotyledons and Dicotyledons, as we have

seen, lateral roots originate in this layer, and, in most Dicotyledons, it helps in the formation of the cambium-layer, and later gives origin to the phellogen.

§ 17. Transition from Root to Stem—the Hypocotyl (p 65).—We have already stated that the vascular system is continuous in root and stem It is evident that the transition from the arrangement characteristic of the root to that characteristic of the stem is effected in that region of the axis which lies between typical stem and typical root This region is the *hypocotyl*

The transition is effected in different ways; but, in many cases, if we trace the vascular tissue from the root to the hypocotyl, we find that each xylem and phloem bundle divides radially into two. These xylem and phloem bundles fuse in pairs to form the conjoint bundles passing up into the stem In this process the phloem bundles practically retain their position with the protophloem towards the exterior, but the xylem bundles twist round so that they lie on the inner side of the phloem bundles with the protoxylem *internal*. In such cases there is the same number of *conjoint* bundles in the stem as there are xylem and phloem bundles in the root

CHAPTER VI.

THE LEAF OF THE ANGIOSPERM

A EXTERNAL CHARACTERS

§ 1 **Parts of the Leaf** (Fig 85) —A leaf is a natural outgrowth on a stem, and arises as a morphologically dissimilar member A *foliage leaf* consists typically of three parts —(*a*) the **vagina** or leaf base (*b*) the **petiole** or stalk (*c*) the **lamina** or blade

The *lamina* is the part of the leaf which is chiefly concerned in the process of carbon assimilation It is usually thin and membranous but in plants which have for various reasons to reduce transpiration and economise their water supply the leaf surface may be much reduced and the leaves become cylindrical (Onion) stiff and pointed (Gorse) or if water is stored up fleshy and succulent (Stonecrop) Occasionally the lamina is wanting altogether as in many scale leaves and in phyllodes (p 147)

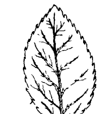


Fig 85 —A TYPICAL LEAF

The *petiole* is typically a cylindrical structure, but its upper surface is usually somewhat flattened, and in many leaves, is grooved or channelled at the base, forming a sort of gutter which serves to draw off water from the leaf Occasionally the petiole is expanded laterally into a membrane or wing (Fig 99) The main function of the petiole is to raise the lamina, and expose it as advantageously as possible to suitable illumination.

It is absent in most Monocotyledons and also in many Dicotyledons.

The *leaf-base* may be regarded as the flattened base of the petiole. In many leaves it is poorly developed, but frequently it forms a sheath round the stem. In Grasses the sheath is long and tubular and supports the base of the internode (Fig. 86, E). Occasionally (as in the Sensitive Plant or Lájvantí) the leaf-base becomes thick and fleshy, and forms an irritable cushion of tissue (the *pulvinus*), which reacts to various external stimuli. Owing to this the leaf can alter its position and is protected from various injurious influences. In many Dicotyledons, rarely in Monocotyledons, the leaf-base bears a pair of outgrowths called **stipules**, representing a development of its membrane or wing (Fig. 86, B).

§ 2. **Various Types of Leaf Structure.**—The forms of leaves are innumerable in correlation with the diverse functions they perform. Several well-marked types, however, are of general occurrence amongst the Angiosperms. They are as follows:—

(*a*) **Cotyledons.**—These have already been discussed. If they come above ground as the first assimilating leaves of the plant, they are much simpler in form than the foliage leaves developed later.

(*b*) **Scale Leaves** (*Cataphylls*).—Typically these are small, brown, membranous leaves devoid of chlorophyll. They are developed on many underground stems (*e g.* rhizomes), and form the protective scales of many buds (Fig. 46, B). Their function is usually protective. They may serve to protect buds that are developed in their axils, or, in the case of bud-scales, they protect the inner undeveloped foliage leaves of the bud. In most cases they represent leaf-bases, petiole and lamina being absent, *e g.* on many rhizomes, and in buds of Horse Chestnut and Sycamore; but bud-scales may be the stipules of foliage leaves (Banyan), or the stipules of scales (Beech and Oak) or rudimentary laminae (Lilac). The nature of bud-scales can be made out by examining the opening buds in Spring. Sometimes scale leaves store food, as in many bulbs.

(*c*) **Foliage Leaves.**—The ordinary green leaves are the chief assimilating, respiring, and transpiring organs of the plant (p. 15). Chlorophyll is present because it is an essential factor in the assimilation of carbon.

(*d*) **Bracts** and **Floral Leaves.**—These are the specialised leaves borne on the reproductive shoots (floral region of the plant). They will be fully considered in connection with the Flower (Chapter IX.).

In §§ 3 to 15 we shall consider more especially the characters of ordinary foliage leaves.*

§ 3. **General Descriptive Terms.**—If the leaf-base is winged and forms a sort of sheath clasping the stem half round at the insertion of the leaf, the leaf is said to be **semi-amplexicaul**; if it clasps completely round, **amplexicaul** (Fig. 86, D). If the petiole is present, the leaf is **petiolate** or stalked; if absent, **sessile**. The leaf is **peltate** if the petiole is attached to its lower surface and not to its basal margin (*e g* Garden Nasturtium—Fig. 86, A). In *sessile* leaves, if the winged leaf-base (continuous with the lamina) clasps round the stem, the leaf is **auriculate** (Fig. 87, B), if it fuses on the other side of the stem so that the stem seems to have grown up through the leaf, **perfoliate** (Fig. 87, A). If there are two opposite leaves at the node, and their membranous bases fuse round the stem, they are said to be **connate** (Fig. 87, C). If in a leaf the membrane runs vertically down the stem for some distance, the leaf is **decurrent** (Fig. 86, C). In Grasses a ligule (see p 60) is developed on the base of the lamina, and the leaf is said to be **ligulate** (Fig. 86, E).

A leaf is **stipulate** or **exstipulate** according as stipules are present or absent. Stipules vary much in position, colour, size, and form. Sometimes they are large, green, and leafy (Fig. 88, B), showing the same development as an ordinary lamina (*e.g.* in the Pansy); in this case they help in the work of carbon-assimilation. When the stipules are dry, small, pale, and membranous they are usually functionless. In some buds (*e. g.* in the Banyan), as already stated, they form the outer protective scales which fall off as the leaves expand. Occasionally the stipules are modified into spines, as in *Zizyphus Jujuba* (the Ber or Bor) and *Acacia arabica* (Babúl), or tendrils (*Smilax*).

Various kinds of stipules are recognised. If they run up the base of the petiole for some distance, they are called *petiolar* (Rose—Fig. 88, A). Where there is only one leaf at the node, if they run

* Much that is given in §§ 3-15 is intended for reference only; the descriptive terms can only be gradually acquired by practical work.

round to the other side of the stem and fuse there, an *opposite* stipule is formed (Banyan); if their inner margins cohere between the leaf and stem, an *axillary* stipule is formed, if they cohere in both ways, a tubular sheath called an **ochrea** (Fig 89) is formed

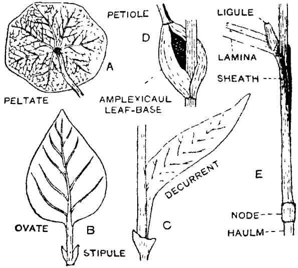


FIG 86 —FORMS, ETC, OF LEAVES.
A, Peltate leaf of Garden Nasturtium; E, Ligulate leaf of a Grass. (Haulm = Culm, p. 77)

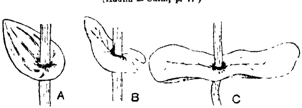


Fig 87.—A, PERFOLIATE LEAF, B, AURICULATE LEAF; C, CONNATE LEAVES.

round the base of the internode (this is characteristic of plants belonging to the Order Polygonaceæ) Sometimes the stipules of opposite leaves (two at a node) fuse on each side to form *interpetiolar* stipules, as in the Rubiaceæ.

§ 4 **Insertion of the Leaf.**—The point at which the leaf base joins the stem is called the *insertion of the leaf*. Leaves are

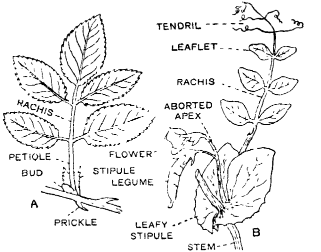


Fig 88.—A, Compound Leaf of Rose with Petiolar Stipules; B, Part of Flowering Shoot of Pea, showing Compound Leaf in which the Upper Leaflets are modified into a Tendril.

described as *cauline* or *ramal* according as they are developed on the main stem or on the branches. Leaves developed on very short "reduced" stems (p 83) so that they appear to come off from the root are called *radical* leaves, as, for example, in Turnip, Carrot, etc.

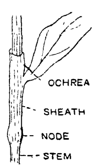


Fig. 89.—Leaf and Portion of Stem of *Polygonum.*

§ 5. **Phyllotaxis** (the arrangement of leaves on a stem)—Two kinds of phyllotaxis are recognised:—(*a*) **Spiral**, (*b*) **cyclic** or *whorled*. In spiral phyllotaxis the leaves are developed one at each node, and are said to be **alternate** (Fig 46, A) It is spoken of as the spiral arrangement, because, if an imaginary line were supposed to pass through the bases of the

leaves in the order of their development, it would describe a spiral round the stem. In cyclic phyllotaxis two or more leaves forming a *whorl* (p. 80) are developed at each node; if two, the leaves are **opposite**; if more, **verticillate.** If in any one whorl the opposite leaves are placed immediately above those in the whorl below, so that there are only two *rows* of leaves on the stem, they are said to be opposite and **superposed.** Usually, however, they are placed at right angles, so that there are four rows of leaves, this is the opposite **decussate** arrangement.

The following facts with regard to phyllotaxis are interesting. In spiral phyllotaxis the imaginary spiral line, following the order of development of the leaves, is called the **genetic spiral.** The angle of circumference between any one leaf and the next in order above it, in other words, the angle between the two *vertical* planes passing through these two leaves, is the **angle of divergence.** Thus, suppose the alternate leaves are arranged in two opposite vertical rows Evidently the divergence, or circumferential distance between any two leaves taken in order, is $\frac{1}{2}$, i e the angle of divergence is 180°. The two vertical rows of leaves are called **orthostichies.**

Again, suppose, calling a particular leaf No. 1, you pass through five leaves before coming to one, No 6, lying immediately above No 1, and that to reach No 6 you have passed twice round the stem. Evidently the divergence is represented by $\frac{2}{5}$ (the whole circumferential distance divided by the number of leaves), and the angle of divergence is 144°. The whole course gone through from leaf 1 to leaf 6 constitutes a *cycle.* There are five rows of leaves or orthostichies. Thus to find the divergence simply divide the number of turns in a cycle by the number of leaves passed on the way or by the number of orthostichies For example, in a divergence of $\frac{1}{3}$, it is leaf No. 4 which lies above No 1, and only one turn of the circumference is gone through; there are three orthostichies.

The divergences common in plants may be arranged in two series :—(a) $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$ . . (b) $\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{9}$, $\frac{3}{14}$, $\frac{5}{23}$ . . The student should notice the peculiar relation existing between the members in each series Each fraction may be got by adding the numerators and denominators of the two preceding ones Thus the series are easily remembered The first series is the more important

In cyclic phyllotaxis there is probably a number of genetic spirals running round the stem; thus, in the opposite decussate arrangement, two with a divergence of $\frac{1}{4}$

§ 6. **Venation.**—The vascular bundles which pass into each leaf from the stem branch out in the lamina and form the veins of the leaf. The veins not only convey watery solutions absorbed by the roots to the various parts of the leaf, and collect the elaborated products, but they also have an important function in giving strength and support to the lamina, whose flattened form is an adaptation to the conditions of carbon-assimilation.

If the lamina is comparatively thin and membranous, we can recognise one or a number of chief veins as they give rise to projecting ridges or ribs on the under surface. But between these there are innumerable small veinlets running through the ground-tissue of the leaf and forming no projecting ridges. The character of the venation, *i e.* the arrangement or appearance presented by the veins, depends chiefly on the number of prominent veins or ribs and the arrangement of the smaller veins or veinlets.

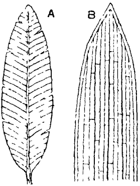


FIG 90 —PARALLEL VENATION A, Unicostate, B, Multicostate

Two chief types are recognised in Angiosperms · — (I) **Reticulate venation,** characteristic of dicotyledonous leaves, though occurring also in a few Monocotyledons, (II) **parallel venation,** found in Monocotyledons only. In reticulate venation the veinlets between the larger veins run together irregularly to form a network (Fig. 86, A). In parallel venation the larger veins or the veinlets all run more or less parallel; no irregular network is formed (Fig. 90)

In both types the venation may be **unicostate** or **multicostate,** according as there is one chief vein (forming the midrib) or a number of chief veins. The former is also spoken of as the feather or pinnate type of venation In multicostate venation the large veins may be *divergent* or *convergent* as they run towards the apex.

I. **RETICULATE VENATION.**

1. **Unicostate** (feathered or pinnately veined), Fig 85.
2. **Multicostate:**
   - (a) **Divergent** (radiately or palmately veined), Fig. 91.
   - (b) **Convergent** (not common).

II **PARALLEL VENATION.**

1. **Unicostate** (feathered, pinnate or curved-veined), e g Banana and Fig 90, A.
2. **Multicostate** (straight-veined):
   - (a) **Divergent:** Many Palms
   - (b) **Convergent:** Grasses, Lilies, Fig. 90, B.

The arrangement of veins in a leaf blade may be regarded as a branch-system Thus the unicostate type is clearly a racemose branch system; while the multicostate type is a cymose branch-system, in which the median rib of the series (*a*, Fig. 91) represents the parent-axis, and those to the side (*b*, *c*, *d*) a number of daughter axes as strongly or almost as strongly developed.

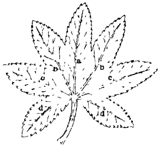


FIG 91 —PALMATIFID LEAF, ILLUSTRATING MULTICOSTATE VENATION AND BRANCHING.

§ 7. Simple and Compound Leaves.

—The appearance presented by the lamina depends chiefly on the extent to which its membrane is developed *between the branches* of the vascular system Sometimes it is completely developed, and the margin of the lamina is entire (Fig. 86, B). Usually, however, it is not completely developed The extent to which it is incomplete varies immensely. Sometimes there are only small irregularities or cuttings of the margin, as in Figs 85, 93 A; frequently larger indentations called *incisions* are produced between the chief veins or branches.

When the wing or membrane is not developed at all between the branches, the leaves are *compound* All other leaves, in which the membrane is present to some extent, however little, between the branches, are ***simple leaves***.

A compound leaf is one in which the lamina is broken up into a number of *separate* parts called leaflets, articulated at one point, or borne on a common stalk or rachis. **A simple leaf** is one in which the lamina is not split up into distinct leaflets The leaflets of compound leaves in many respects resemble simple leaves.

In the case of trees large leaves are frequently much divided or compound. The significance of this is partly that the leaves are thus protected from mechanical injury, more especially from the destructive action of wind. This can be recognised by comparing the leaves of such trees with the leaves of the Plantain (*Musa*) during a storm. But, apart from this, the subdivision of the lamina also prevents overshading of the lower leaves borne on the plant. This is probably the chief reason why large leaves borne on many herbaceous plants are much divided or compound.

The leaves of aquatic plants are often much divided The reason in this case is partly that the leaves are thus preserved from risk of mechanical injury; but the chief reason is that, being much divided, the leaves present as large a surface as possible to the water, and are therefore able to carry on more efficiently the processes of respiration and carbon-assimilation.

§ 8. **Outline of the Lamina.**—Many terms are in use to describe the simpler forms of outline presented by simple leaves or the leaflets of compound leaves. Only those most frequently used are given below.

A leaf is **subulate** (Fig 92, A) when it is narrow, firm, and hard, and gradually tapers from base to apex, ending in a sharp point, as in the Gorse; **acicular**, if it is elongated and sharp-pointed, with distinct edges (Fig 92, B); **linear**, if elongated, flattened, and membranous, with parallel margins as in Grasses (Fig 92, C); **lanceolate**, if elongated and gradually tapering towards base and apex (Fig 92, D); **oval**, or **elliptical**, if relatively shorter and broader, tapering towards base and apex (Fig 85); **oblong**, if of much the same length and breadth, but rounded at base and apex (Fig 92, E); **orbicular**, sub-rotund, or rounded, if it approximates towards the circular (Fig 86, A); **ovate**, if rounded off towards the base and pointed towards the apex (Fig. 86, B); **obovate**, if the reverse (Fig 92, G); **cordate**, or heart-shaped if pointed at apex and notched at the base where the petiole is attached (Fig 92, F); **obcordate**, if notched at apex and tapering towards the petiole at the base (Fig. 92, H); **reniform**, or kidney-shaped, if notched at the base, more or less elongated transversely, and *rounded* at the apex (Fig. 93, A); **spathulate**, if wide and rounded at the apex and *gradually* narrowing towards the base (Fig. 93, B); **cuneate**, or wedge-shaped, if

similar to the spathulate form, but with a more or less acute or drawn-out apex (Fig 93, A); **sagittate**, if shaped like an arrowhead, with the two basal lobes directed backwards (Fig 93, C);

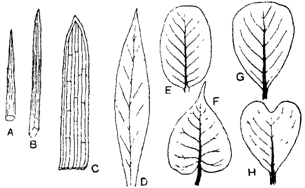


Fig 92 —Outlines, etc, of Leaves

A, Subulate, B, Acicular, C, Linear, D, Lanceolate, E, Oblong, F, Cordate, G, Obovate, H, Obcordate In E and G the apex is rounded or obtuse, in F, acuminate, in H, retuse

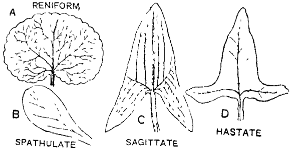


Fig 93 – Outlines of Leaves.

hastate, or halbert-shaped, if the two basal lobes are directed outwards (Fig 93, D) Sometimes the two halves of a leaf are not equally developed (*e.g* in *Begonia*) Such leaves are *oblique*. They would be described as obliquely cordate, obliquely ovate, etc.

Sometimes the outline is best indicated by a combination of the above terms; thus **ovate-lanceolate,** etc.

§ 9. **The margin** of a leaf or leaflet is **entire** if it is perfectly even and shows no irregularities (Fig. 92); **serrate,** if it shows a number of sharp processes directed forward towards the apex (Fig. 88, A); **dentate,** or toothed, if these processes project outwards and are not directed forwards (Fig. 96, C); **crenate,** if the processes are rounded (Fig. 93, A); **biserrate, bidentate, bicrenate,**

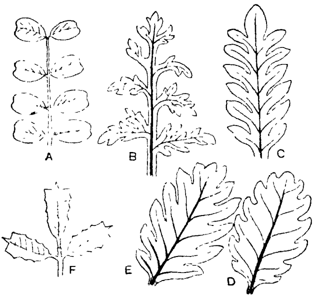


Fig. 94.—Incision of Lamina.

A, Paripinnate compound leaf, B, Pinnatisect leaf, C, Pinnatipartite leaf E, Pinnatifid leaf, D, Leaf with sinuate margin, F, Imparipinnate unijugate compound leaf.

if the processes themselves bear smaller secondary processes of the same kind; **spiny,** if the margin bears a number of hard, spiny processes resembling prickles (*e.g.* Holly); **crisped,** or *curled,* if very wavy and irregular, as in the Endive; **sinuate,** if the margin is more deeply indented, as in the Oak (Fig. 94, D). The sinuate margin forms a transition to the deeper cuttings of the margin, which are called incisions (§ 12).

§ 10 **The apex** of a leaf or leaflet may be **rounded** (or obtuse —Fig 92, E); if it comes to a point, it is **acute** (Figs. 92 c, 88 A); if slender and very much drawn out, **acuminate** (Fig 95, A); if it seems to have been cut across, **truncate**; if it bears a *distinct* minute, pointed process, **mucronate** (Fig 94, F); if there is a rounded depression at the apex, **retuse** (Fig. 94, A); if the depression is sharp, **emarginate.**

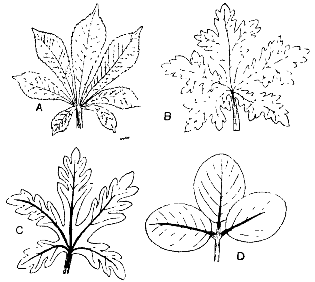


Fig 95 —INCISION OF LAMINA.
A, Multifoliate palmate compound leaf, B, Palmatisect leaf, C, Palmatipartite leaf, D, Ternate compound leaf

§ 11 **Hairs.**—The leaf may be hairy If the margin of the leaf bears a fringe of fine hairs, it is described as **ciliate.**

§ 12 **Incision of the Lamina.**—In a *unicostate* leaf, if the incisions do not pass half-way down to the midrib, the leaf is **pinnatifid** (Fig 94, E), if rather more than half-way, **pinnatipartite** (Fig. 94, c); if *almost* to the midrib, **pinnatisect** (Fig 94, B) Corresponding to these simple

leaves, we have, where the incision is complete, the compound leaf of the **pinnate** type (Fig. 94, A). Similarly, where the venation is multicostate, we may have **palmatifid** (Fig. 91), **palmatipartite** (Fig 95, C), or **palmatisect** (Fig. 95, B) simple leaves; and the corresponding compound leaf is of the **palmate** type (Fig. 95, A).

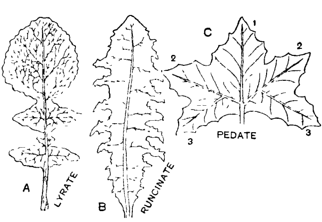


Fig 96—FORMS OF LEAVES
In C the numbers indicate the branching

The terms pinnati-fid, -partite, -sect, palmati-fid, -partite, -sect are also applied to leaflets of compound leaves. If the divisions of a simple leaf are again incised, the terms **bi-pinnatifid**, etc, are used; or a pinnatipartite leaf may have divisions which are pinnatifid, etc.

When a unicostate leaf is incised in such a way that there is a large *rounded* terminal division with others which become gradually smaller towards the base, the leaf is said to be **lyrate** (Fig. 96, A). A **runcinate** leaf (*e g.* Dandelion, Fig. 96, B) is a pinnatifid leaf in which there is a large pointed terminal lobe, and the apices of the smaller lobes behind are directed backwards In a multicostate leaf, where, as already indicated, the branching is of the cymose type, only daughter-branches of the first order, as a rule, are given off in a cymose fashion, as in Fig 91; but occasionally these may again branch cymosely, as in Fig 96, C. This is known as a **pedate** leaf.

§ 13. **Compound Leaves.**—Often a compound leaf is mistaken by beginners for a stem bearing leaves. The following points of difference should be carefully noticed:—(a) a compound leaf has no apical bud or growing-point, (b) it has a bud in its axil, and does not arise in the axil of a leaf; (c) it may have stipules, or an expanded sheath at the base, (d) the *apparent* leaves (really leaflets) have no axillary buds

There are certain special terms used in the description of compound leaves to which we must now refer In the *pinnate leaf* the leaflets are borne on the common rachis or axis. Usually the leaflets are arranged in pairs, the leaflets of each pair being opposite each other. If an unpaired terminal leaflet is present, the leaf is

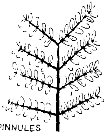


Fig 97 —Bipinnate Leaf

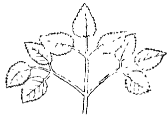


Fig 98 —Biternate Leaf

described as **imparipinnate** (Fig 88, A); if no terminal leaflet is present, so that the number of leaflets is even, the leaf is **paripinnate** (Fig 94, A) If there is only one pair of leaflets, the leaf is *unijugate* (Fig. 94, F); if two, *bijugate* (Fig 88, A), etc. Sometimes pairs of large leaflets alternate with pairs of small leaflets Such a leaf is said to be *interruptedly pinnate* (Potato) The leaflets themselves may be completely incised Here the secondary leaflets formed are called **pinnules**, and the leaf is said to be *bipinnate* (Fig. 97) If these again are completely incised, the leaf is *tripinnate* Usually, however, the upper leaflets in a bipinnate or tripinnate leaf are incompletely incised, and either pinnatifid or pinnatipartite

In a *palmate* compound leaf the leaflets come off at the same point. If there are two leaflets, the leaf is *bifoliate*, or *binate*, if three, *trifoliate*, or *ternate* (Fig 95, B), and so on, if a large number, *multifoliate* (Fig 95, A). The ternate leaf resembles the imparipinnate unijugate leaf Usually leaves with three leaflets are

regarded as ternate, except where, as in Fig. 94, F, the secondary petioles come off at different points. Fig. 98 shows a biternate leaf.

In the Orange there is a peculiar compound leaf, bearing only one leaflet. This is recognised as a compound leaf by the fact that the expanded lamina is distinctly articulated to the winged petiole (Fig. 99).

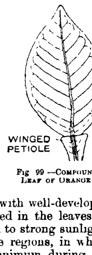


Fig. 99.—COMPOUND LEAF OF ORANGE

§ 14. **Texture and Duration of Leaves.**—The texture and duration of leaves depend largely on the nature of the environment and the adaptation of the plant. Shade- and moisture-loving plants have thin leaves with poorly developed epidermis. Sun-plants and plants living in dry conditions, in which there is often a risk of excessive transpiration, usually have firmer and thicker leaves with well-developed cuticle. This condition is very marked in the leaves of many tropical plants which are exposed to strong sunlight, and in evergreen plants in temperate regions, in which transpiration must be reduced to a minimum during the winter season.

Leaves which are thin and membranous are described as *herbaceous*. Firm, thick leaves are called *coriaceous*. Some are succulent and *fleshy*. The leaves are *caducous* if they fall off very early; *deciduous*, if they fall at the end of each season; *persistent*, if they remain on the plant for more than one season. Plants with persistent foliage leaves are *evergreens*.

§ 15. **Prefoliation.**—The form and arrangement of the young leaves in the bud condition, for which the term prefoliation is used, show a beautiful regard for economy of space. Prefoliation includes (*a*) *Ptyxis*, or the form of the young leaves *in the bud*, *i.e.* the way in which they are folded or rolled on themselves; (*b*) *Vernation*, or the relation between the different leaves in the bud, *i.e.* the manner in which they are arranged with regard to each other. These points may be determined either by removing the leaves of a bud one by one, or, better, by taking cross-sections of the bud. In flower-buds we speak of **prefloration**, including **ptyxis** and **æstivation**.*

* The terms vernation and prefoliation, æstivation and prefloration, are variously used by different writers.

(*a*) **Ptyxis of the Leaf** (Fig 100). It is *plane* if there is no folding or rolling at all, *conduplicate*, if the right half is folded over on the left, *plaited*, or *plicate*, if there are numerous longi-

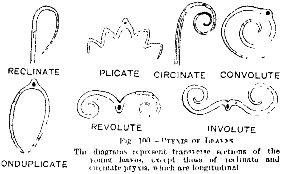


Fig 100 – PTYXIS OF LEAVES
The diagrams represent transverse sections of the young leaves, except those of reclinate and circinate ptyxis, which are longitudinal

tudinal folds; *crumpled*, it folded in all directions, *convolute*, if rolled from one margin to the other, *involute*, if rolled from both margins to the middle of the upper surface, *revolute*, if rolled

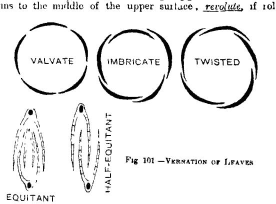


Fig 101 —VERNATION OF LEAVES

similarly to the middle of the lower surface; *circinate*, if rolled up from apex to base

(*b*) **Vernation** (Fig 101) is *valvate* if the young leaves touch each other laterally, but do not overlap; *imbricate*, if some overlap

others, but not regularly; *twisted*, or *contorted*, if one margin of each leaf is directed inwards, and is overlapped, while the other margin is directed outwards, and overlaps the margin of the adjacent leaf.

§ 16 **Special Adaptations of Leaf Structure.**—Many striking modifications of foliage leaves have arisen in adaptation to special conditions.

(*a*) **Leaf Tendrils.**—Leaves or parts of leaves frequently have the form of tendrils (p 83) Thus in the Pea the tendrils represent the leaflets of a compound leaf (Fig 88, B) In some species of Pea, e g *Lathyrus aphaca*, all the leaflets are specialised in this way, and the functions of the foliage leaf are taken on by the stipules, which are large and green The stipules may be modified into tendrils, as in Smilax

(*b*) **Leaf Spines.**—Leaves or parts of leaves may take on the form of spines In many cases this modification must be regarded as primarily due to the necessity for cutting down transpiration, but spines also serve as protective organs The whole leaf may be thus modified, as in the Barberry, where the spines are branched In the Barberry intermediate forms between foliage leaves and spines are often found. In the Gorse the leaves as well as the branches are modified into spines The young seedling Gorse bears trifoliate leaves In the Orange the thorns represent the first leaf of an axillary branch In *Zizyphus Jujuba* the stipules are spiny, and the same is the case in the Korukapuli (*Pithecolobium dulce*) and in the Babúl

(*c*) **Phyllodes**—In some Australian Acacias the lamina of the leaf is absent, while the petiole develops a wing and takes on the appearance and functions of a lamina These flattened petioles are called *phyllodes* and are an adaptation to dry conditions. They are vertically expanded, with surfaces right and left, instead of horizontal as in ordinary bifacial leaves This vertical position, together with the reduced surface exposed to the air, diminishes transpiration The young seedling Acacias have normal compound leaves, and the transition from these to phyllodes can be observed during the growth of the seedling

(*d*) **Pitchers, etc.**—Various interesting modifications of leaves are found in insectivorous plants. The most striking example perhaps occurs in *Nepenthes*, the Pitcher Plant, where the leaves are modified into pitcher-like organs. An account of insectivorous plants is given in Chapter VII

[*Note*:—*For directions with regard to the description of leaves see Appendix*]

B INTERNAL STRUCTURE OF THE LEAF

§ 17 **The Petiole.**—A stout petiole or leaf-stalk, when examined by itself, *i e* without its lamina, might be mistaken by the student for a stem As a rule, however, it is readily distinguished In most cases the petiole is a dorsiventral structure, it is not perfectly cylindrical, but more or less flattened, often markedly grooved on its upper surface

In Angiosperms one or more collateral bundles pass from the stem into the leaf (p. 95). They are accompanied by a tissue continuous with the pericycle and endodermis. Usually, as they run through the petiole, they break up into a number of smaller collateral bundles, each of which becomes surrounded by pericycle and endodermis These, as seen in transverse section, may be scattered more or less irregularly with their xylem portions towards the middle of the upper surface, or in a curved band Occasionally (*e g* the Horse Chestnut) they form a ring, as in the stem of the Dicotyledon—their xylem portions being towards the middle of the petiole Even in this case it is usually found that the bundles towards the upper surface are smaller than those towards the lower surface.

The pericycle and endodermis, though present, are as a rule not very distinctly marked off from the surrounding ground-tissue Sclerenchyma may be developed in the pericycle The rest of the ground-tissue is mostly parenchymatous, but bands or ridges of collenchyma or sclerenchyma are frequently developed beneath the epidermis The epidermis resembles that of the stem.

In dicotyledonous petioles a rudimentary cambium is present between xylem and phloem. It is only in a few exceptional cases that it becomes active and gives rise to secondary growth.

§ 18 **The Lamina—bifacial type.**—A section (Fig. 102) through a small portion of the lamina of an ordinary bifacial leaf (p. 11) at right angles to one of the veins shows

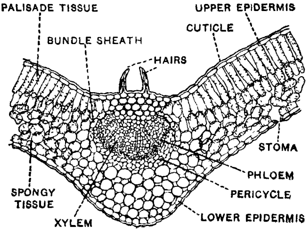


Fig 102 —LEAF
Transverse section taken at right angles to the midrib.

a well-marked **epidermis** with cuticle protecting the upper and lower surfaces. Between these is the ground-tissue or **mesophyll** of the leaf, with the vascular bundles running through it.

Towards the upper surface the mesophyll consists of one or more layers of columnar or elongated cells, with comparatively few intercellular spaces, and arranged more or less at right angles to the epidermis. This is the **palisade** parenchyma. Towards the lower surface the mesophyll consists of smaller, rounded or stellate cells loosely packed

together so that there are numerous intercellular spaces communicating with stomata in the lower epidermis. This is the **spongy** parenchyma The cells of both palisade and spongy mesophyll contain numerous chloroplasts. The palisade tissue is concerned chiefly in the work of carbon-assimilation, the spongy tissue also discharges that function, but is more especially adapted to allow interchange of gases and vapour between the atmosphere and the leaf-tissue

Between the palisade and spongy mesophyll run the vascular bundles In the diagram one of the veins has been cut transversely It consists of **xylem** towards the upper surface, **phloem** towards the lower Some of the smaller bundles may be cut obliquely or longitudinally *Endodermis* and *pericycle* are present round the larger bundles, but are usually recognisable as distinct layers only when, as frequently happens, the pericycle is lignified and the endodermal cells contain starch (starch-layer) The pericycle disappears in the smaller veins

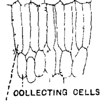


Fig 103—Part of Section of Leaf, showing Palisade and Collecting Cells

In many leaves it can be seen that the palisade cells at their inner ends are connected in groups with single mesophyll cells (Fig 103). The latter are called **collecting cells** because they collect the carbohydrates elaborated in the mesophyll tissue, and pass them on to the cells of the bundle sheath whose function apparently is to conduct the carbohydrate material from the leaf downwards into the stem

The structure of the leaf varies considerably in detail according to its adaptation The palisade tissue is well developed in the leaves of plants which grow exposed to bright sunlight, it is poorly developed in shade-plants. In the mesophyll strengthening bands of **sclerenchyma** may here and there be developed, usually between the vascular bundles and the epidermis. This is well seen in

Grasses. Cells containing crystals or cavities containing oil are frequently found. In some thick coriaceous leaves (*e g* Holly) a hypodermal layer is developed serving probably for water storage.

In many monocotyledonous leaves which stand more or less erect, as, for example, in various Lilies, palisade tissue is not developed. The mesophyll tissue presents the same appearance towards both surfaces and consists of small rounded cells containing chloroplasts The bifacial character of the leaves, however, is shown by the fact that the xylem portions of the vascular bundles are all directed to the same surface (upper surface).

§ 19 **Isobilateral and Centric Leaves.**—In the isobilateral leaf of the Iris palisade tissue is not developed, and the mesophyll presents the same appearance towards both surfaces There is a series of bundles towards each side, the phloem portions of the bundles in each series being directed outwards towards the epidermis The lower part of the leaf is V-shaped in section (Fig. 102)

In centric leaves there is a radial arrangement of tissue.

§ 20. **Development of the Leaf** (Figs 63, 64) —The leaf originates as a small lateral protuberance at the meristematic apex of the stem This protuberance consists of dermatogen and periblem only. The development is superficial, and therefore **exogenous** (p 113). At first all the cells are meristematic, but later the meristematic tissue is restricted to the middle or base of the developing leaf, and growth is therefore *intercalary*. Finally, when the full number of cells has been produced, the meristem dies out. At this stage the young leaf is still very small and folded up in the bud with the other leaves.

The expansion and increase in size of the leaf, when the bud unfolds, is due simply to the growth of the individual cells, not to the formation of new cells During the earlier development procambial strands make their appearance (developed here in periblem-tissue), which sooner or later become connected with the procambial strands of the stem. These differentiate into the vascular bundles.

§ 21. **Leaf Apex—Endings of the Veins.**—It will be evident from the foregoing paragraph that the fully formed leaf has no apical growing-point such as the stem has, and further, therefore, that the terminations of the vascular bundles or veins must be different. Frequently the veinlets have no definite endings, but form anastomoses or fusions with neighbouring veinlets Sometimes they end blindly in the mesophyll. Where the ending is definite, the vascular tissue is gradually lost. The larger xylem vessels and phloem elements disappear The remaining small xylem elements are of the nature of spiral and reticulate tracheides. In a few cases these pass gradually into a mass of small-celled glandular tissue (*epithem-tissue*), with which are usually associated a number of water-pores (p 60).

§ 22 **Fall of Leaves.**—There are certain important processes connected with leaf-fall in deciduous trees. Before the leaf falls a layer of cork is formed across the base of the petiole by the meristematic activity of the living cells (phellogen) lying immediately internal to it This meristematic property is taken on, not only by cells of the ground-tissue of the petiole, but also by cells in the vascular bundles, so that the cork-layer is formed right across the petiole, and joins on to the cork-layer formed in the stem. The fall of the leaf is directly due to the disorganisation of the layer of parenchymatous cells (**absciss-layer**) lying just outside the cork-layer. Thus the surface exposed when the leaf falls is protected by the cork-layer. The wood-vessels of the vascular bundles are constricted by the cork-layer, and may also be closed with gum, so that when they are broken across there is no exudation of sap

Leaf-fall is determined by interruption or failure of the water-supply produced by conditions which either retard the absorption of water by the root or unduly promote transpiration. Thus leaves fall naturally in this country towards the approach of winter, but a long period of very hot, dry weather may bring about the same result. That it is a natural process, due to vital activity, is shown by

the fact that the leaves of a dead branch do not fall. There is a similar formation of cork at the base of prickles.

§ 23 We may conveniently close the chapter with a *general* definition of a leaf. A leaf may be defined as any natural exogenously developed outgrowth of a stem, differing from the stem itself in structure, occupying a definite position in development, and having in different regions a form and organisation adapted to the functions it has to perform. A leaf-structure, whatever its special form, is distinguished from a stem or root by its position and mode of development

CHAPTER VII.

NUTRITION AND GROWTH.

§ 1. In Chapter I (§ 11) we indicated, in a very general way, the physiological processes connected with nutrition and growth, and here and there we have made scattered references to the functions of various tissues and organs. We have now to give special consideration to these processes as they are exhibited in the higher plants Although considered with special reference to the Angiosperm, they are essentially the same in all green plants showing differentiation into root, stem, and leaf Before reading this chapter the student should again refer to pp 12-15

§ 2 **Importance of Water.**—That protoplasm is the essential living substance by which all these physiological processes are carried on has already been sufficiently emphasised We must again allude, however, to the important part played by water Most parts of plants contain a considerable amount of water, occasionally, in very succulent plants, it forms as much as ninety per cent of the total substance All the organic substance is permeated with water Water is one of the important forms in which essential chemical elements (Hydrogen and Oxygen) enter the plant Besides this, it is the medium for the solution, absorption, and transit of all other food materials, the medium by which these are brought into intimate relation with the living substance. Amongst the manifold adaptations exhibited by plants, some of the most striking are concerned with the regulation of the absorption, distribution, and exit of water.

Exp. 1.—Place some dry seeds (*e g* Pea or Barley) in moist sawdust, and others in perfectly dry sawdust, and compare the results after a week or two It will be found that water is necessary for the germination of seeds.

Exp. 2.—Place one or two dry seeds (*e g.* Pea, Horse Bean, or Barley) in a test-tube and heat carefully over a Bunsen flame Observe the moisture which condenses on the sides of the test-tube. The water is driven off more rapidly if the seeds are first of all cut into small pieces. So-called "dry" seeds really contain water.

Cut a number of dry seeds into pieces and weigh them. Place them in a porcelain crucible or basin (also weighed) and dry them thoroughly without charring them. This can be done by means of a water-bath or a sand-bath over a small flame. By weighing again determine how much water the seeds originally contained It is usually a little over 10 per cent. If whole seeds dried in this way are placed in moist sawdust it will be found that they can still absorb water but do not germinate Evidently the water present in seeds is necessary for life, though not sufficient to enable germination to take place.

Exp. 3.—Observe the drooping which takes place if a plant is unwatered or if a branch is cut off and exposed to the sun. The amount of water contained in the succulent parts of plants (leaves, etc) can be determined by the method of Exp 2 It is usually from 60 to 90 per cent, and depends not only on the part examined, but also on its age.

§ 3 **The Food Materials of a Green Plant.**—If we make a chemical analysis of a plant—an analysis of the gases given off, and the residue or *ash* left behind on burning the plant—we recognise the following chemical elements —carbon, oxygen, hydrogen, nitrogen, sulphur, phosphorus, calcium, potassium, magnesium, iron, sodium, silicon, and chlorine, with, frequently, traces of manganese, iodine, and others Of these, only the first six enter into the actual composition of the living substance of the plant. It is evident that all these elements found in the plant must enter it in the food-materials absorbed, *i e* the food-materials consist of, or contain, these elements. We have already indicated (p. 13) that the food-materials absorbed by a green plant are of the nature of simple inorganic compounds, and that they are taken in in solution.

All the carbon used by the plant in the processes of assimilation is derived from the carbon dioxide (CO_2) of the

atmosphere, which is absorbed by the aerial *green* parts of the plant (chiefly leaves) in the presence of light. All the other elements are derived from the water and dissolved mineral substances ("salts") absorbed by the root in the process of **root-absorption.** Dissolved carbon dioxide, or carbon taken in by the root in the form of carbonates, is not made use of in the anabolic processes.

The necessary oxygen* and hydrogen are derived chiefly from water, partly from salts containing these elements. Nitrogen is absorbed in the form of nitrates (for exceptions see pp. 196-202), sulphur in sulphates, phosphorus in phosphates, chlorine in chlorides, silicon in silicates, iron, potassium, calcium, and magnesium form the metallic bases of these salts If substances absorbed are made use of in metabolism, the absorption continues The amount absorbed depends on the amount assimilated

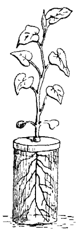


Fig 104 A Plant of Buckwheat grown with its Roots in a Culture-solution

It has been determined by experiment that, for most green plants, the *essential elements*, *i e.* the elements absolutely necessary for *healthy* growth, are carbon, oxygen, hydrogen, nitrogen, sulphur, phosphorus, calcium, potassium, magnesium, and iron. The others are non-essential, or, at all events, are essential only for certain plants

That carbon is essential is shown by the fact that, while a green plant can be grown in a nutritive solution which contains no carbon, it cannot be grown in an atmosphere deprived of carbon dioxide

That the others are essential has been determined by the method of **Water-Culture.** A number of plants of the same species are grown in glass

* Oxygen of respiration is absorbed by all parts of plants, see p 184.

jars, their roots immersed in a nutrient solution of inorganic salts (Fig 104) It is found, with most plants, that there is healthy growth only if the solution contains the elements mentioned in proper form and degree of concentration. Various unhealthy symptoms appear if one or more of them are absent. Thus, if iron is left out, there is no development of chlorophyll, and the presence of potassium is necessary for the formation of carbohydrates The solution must be very dilute.

Exp. 4.—If seeds, seedlings, leaves, or other parts of plants be thoroughly dried, as explained in Exps. 2 and 3, the dry substance that is left consists largely of organic matter and is combustible. If this is thoroughly burned, by heating strongly, a small quantity of ash is left behind By careful weighing the amount of ash can be determined. It is generally about 1 to 3 per cent. of the *total* weight It contains all the metallic elements found in the plant combined in the form of phosphates, sulphates, carbonates, and chlorides Silica is very abundant in the ash of grasses. The composition of the ash in different individuals of the same species varies according to the character of the soil

Exp. 5.—Heat a portion of a Bean-cotyledon, attached to a long needle, in the Bunsen flame until it chars. Rub the charred mass on white paper, it leaves a black mark of charcoal (carbon). Continue to heat the piece for some minutes and note that it burns to ash. Pieces of wood, heated in a tube, are similarly reduced to charcoal, which, if burned, leaves an ash behind

Exp. 6.—Heat a few crushed seeds of Bean or Pea, mixed with soda lime, in a test-tube Ammonia will be given off, proving the presence of nitrogen in the seeds

Exp. 7.—Get some large jars, each holding at least a quart, for water-culture experiments Sachs' solution consists of 2 grammes of potassium nitrate, 1 gramme each of sodium chloride, calcium sulphate, magnesium sulphate, and calcium phosphate, and a drop or two of iron chloride (or iron phosphate) to 2 litres of distilled water Knop's solution, which is perhaps better, consists of 2 grammes of calcium nitrate and 0 5 gramme each of potassium nitrate, magnesium sulphate, and potassium phosphate, with iron as before, in 4 or 5 litres of water The solution should be made up as required.

Grow seedlings of Bean, Pea, Maize, Buckwheat, and other plants until the roots have grown a few inches long, then fix each seedling into a cork The cork should have a hole in the centre for the plant, a slit somewhat narrower than the hole running to the edge of the cork (so that the plant can be removed easily when necessary),

and another hole for a stick to tie the plant to. Take care to keep the cork, as well as the part of the plant which is in contact with it, quite dry; most failures in water culture are due to "damping off" at this part (caused by fungi). If a stick is used to support the plant, there is no need for any packing material; in any case, do not use cotton wool for this purpose, but soft asbestos which has first been heated and allowed to cool.

Darken the roots by covering the jars with black cloth or paper, add distilled water each day to replace that lost by evaporation (using a funnel, and not letting the cork get wet). Once a month take the plant out, wash its roots gently in a basin of water, pour out the culture solution, and let the plant remain with its roots in plain water for two days before placing it into fresh culture solution.

Choose seedlings as nearly equal in size and general growth as possible, then place some in a complete solution, others in a solution from which one or other of the essential elements is wanting. To deprive the plant of potassium, use sodium nitrate instead of potassium nitrate, and calcium phosphate instead of potassium phosphate. Deprive others of calcium by omitting the calcium nitrate; of phosphorus by omitting the potassium phosphate, of magnesium by using calcium sulphate in place of magnesium sulphate; of sulphur by using magnesium chloride instead of the sulphate; of nitrogen by using sodium chloride and calcium sulphate in place of calcium and potassium nitrates; of iron by omitting the iron salt (which should be added in all other cases).

The culture solution should not be alkaline, or the roots suffer; if it turns red litmus to a blue colour, add acid (*e g* phosphoric acid) until it gives an acid reaction. The roots should be supplied with air, the simplest plan is to force air into the solution every day or two with a bicycle-pump or a condensing syringe.

Exp. 8.—Compare the growth of seedlings (of the same kind of plant) which have been supplied with (1) distilled water; (2) tap water, (3) culture solutions (some complete, others with one element or other omitted in each case). If you grow the plants in washed sand instead of culture jars, water with (1), (2) or (3) daily. In either case, compare also with plants grown in good garden soil. After, say, six weeks dry thoroughly and weigh the seedlings, and compare their dry weights; then burn them and compare the ash weights.

§ 4. **Soil.**—A fertile soil must contain the same essential elements as the full culture-solution, and in a form available for use by plants. In a general way, soil may be regarded as an aggregation of organic and inorganic particles. The proportion of organic and inorganic material varies widely in different soils. The decaying organic

matter present is called *humus*, and can be removed by burning The inorganic material consists chiefly of sand, clay, and calcareous matter

Each particle of the soil is surrounded by a film or pellicle of water. This water, which is called the **hygroscopic water** of the soil, is firmly adherent to the particles, just as water adheres to or wets the surface of a glass. It is present even in the driest soil, and can only be completely got rid of by heating the soil to 100° C Between the soil-particles are spaces or interstices which, if the soil is in a good physical condition, are largely occupied by air; but in very damp or water-logged soils they are filled with water—the **free water** of the soil—which can trickle through the soil under the action of gravity. This free water is injurious to plants (except those specially adapted, *e g.* bog- or water-plants) because it interferes with the proper respiration of the root. It is the object of drainage to remove it

Some of the inorganic substance in the soil is dissolved in the hygroscopic water, and it is this water, with its dissolved salts, which is absorbed by the roots of plants Normally, the organic substance is not absorbed by green plants; but, owing to decomposition effected in it by micro-organisms (Bacteria and Fungi, especially Moulds), and leading to the formation of simpler compounds, it serves to replenish the store of inorganic substance, and more especially nitrates, necessary for plants. The composition of the water present in the soil can be learned by analysis of drainage water; and soils can be tested for soluble substances by letting distilled water drain through samples of them, and then applying tests for the essential elements.

The air contained in the soil is constantly being renewed by diffusion from the air above. Since the processes going on in the soil consist largely of oxidation, soil-air is poorer in oxygen and richer in carbon dioxide than atmospheric air.

Sandy Soils are called "light" because they are easy to work; they are more porous, warmer, and drier than clay soils A pure sand contains little but insoluble silica in the form of quartz-grains;

hence it acts only as a sterile medium, though when watered with dilute nutrient solutions many plants are able to grow well in it.

Clay Soils are said to be "cold" because they contain more water than sandy soils, and therefore lose heat more rapidly by evaporation; but all good soils contain more or less clay, which is richer in plant food than any other part of the soil. In drying, clay tends to form a hard compact mass impenetrable by the roots of plants. The presence of clay increases the power of retaining water, which is very deficient in sand, but this makes it difficult for a plant growing in a clayey soil to absorb enough water unless the soil contains a large amount; in the latter case, the soil is badly aerated and hence, for lack of oxygen, the roots are unable to develop to any great extent or to penetrate deeply. Clay is also of great service to plants by fixing various substances essential for plant food, that is, by combining with these substances and preventing them from being too easily washed out of the soil by rain-water.

Calcareous matter supplies plant food in the form of lime, magnesia, and phosphoric acid. It improves the texture of clay soils by making them friable and easily worked. It also acts as a base with which acids, formed by decay of organic matter, can unite and thus be made harmless; if such basic material is absent the soil becomes "sour" through the accumulation of organic acids. Even more important is the part it plays in the process by which certain bacteria convert into nitric acid the nitrogen present in organic matter or ammonia compounds; this process (nitrification—see § 6) occurs only in a weak alkaline solution and the nitric acid unites with the lime.

Humus, the decaying organic matter of the soil, is of great importance both from its physical and chemical properties. It is a light, bulky, dark-coloured substance, with a great capacity for holding water. The presence of humus gives the soil a loose, open texture, and makes it able to absorb and retain water. In woods humus often accumulates to a considerable depth, but in ordinary soils it is only present to a depth of about a yard, and this part of the soil has a looser texture and darker colour than the underlying subsoil, which contains no humus. Humus contains from 4 to 9 per cent. of nitrogen, far more than is present in the vegetable matter from which the humus is produced. The conversion of vegetable matter into humus is helped by bacteria, moulds, earthworms, caterpillars, etc.

Exp. 9.—Get about a pound of garden soil, stir it up in water to form a paste, place this in a jar, fill the jar with water, cork it, shake well for a few minutes, then allow to stand till the soil settles to the bottom. Examine the soil after it has settled; the coarser material at the bottom is *sand*, above this is finer material consisting chiefly of *clay* (the finer grains remain suspended in the water, making it cloudy), and on top of the water floats a little decomposed vegetable matter (*humus*).

Exp. 10.—To compare the *absorption of water by different soils*, take 100 grammes of gravel, sand, rich loam (good garden or field soil), leaf mould, and dry, powdered leaves, and put each sample into a wide tube—*e g.* a lamp chimney—closed at the lower end by a bored cork ; a glass funnel will do instead. Hold each tube or funnel in turn over a tumbler, and pour into it a litre of water ; then measure the water that runs out at the bottom in each case Which sample absorbs and retains most water and therefore allows least water to run through? In an experiment like this the weight in grammes of the water absorbed by 100 grammes of each dry sample was. gravel, 6; sand, 30; barren sandy soil, 35; rich loam, 70; leaf-mould, 220, leaves, 500. These results show clearly that the water-absorbing capacity of soils is greatly increased by the presence of vegetable matter.

Exp. 11.—Pack clay or garden soil into a glass funnel, then pour in some ammonia-water, and place the funnel over a tumbler. The water will, if the clay is packed tightly enough, come out at the bottom without any smell of ammonia The ammonia has been absorbed by the silicate of alumina present in the clay.

§ 5. **Root-Absorption.**—The water of the soil with the substances dissolved in it is absorbed by a process of **osmosis.** This may be regarded as a simple physical process, modified in the case of root-absorption by the vital activity of the protoplasm. It may be defined as diffusion *through a permeable but non-porous membrane.*

If we place in a vessel of water a bladder filled with a strong solution of a substance having an attraction for water (an osmotically active substance, *e g* sugar), a *large* amount of the water will diffuse (pass by osmosis) into the bladder (*endosmosis*), while a *small* amount of the solution will diffuse out (*exosmosis*) The weaker fluid diffuses faster and thus continues until the same concentration is acquired, when it is equally rapid in both directions, and hence apparently ceases It should be noticed, also, that, in the above example, a considerable pressure will be set up inside the bladder, owing to rapid endosmosis. This has an important application in connection with root-absorption.

The root-hairs are the absorbing organs. There is very little absorption by the surface of the root itself The hairs come into close contact with the particles of the soil and, like the particles, are invested by films of water.

The wall of the root-hair, *together with the primordial utricle*, is the osmotic membrane, outside this is the hygroscopic water, with various salts in *very weak* solution, inside is the cell-sap, a *comparatively* strong solution, containing many organic compounds with a strong affinity for water (probably the most important of these in this connection are sugars and organic acids) The primordial utricle exercises an important influence on the process by preventing the diffusion of certain substances which could readily diffuse through the wall of the hair alone Further, it allows only very weak solutions to pass through and retains the water in the vacuole *even at a high pressure*, thus bringing about a very tense or *turgid* condition of the cell (cf the distension of the bladder).

Thus in root-absorption a very large amount of hygroscopic water with dissolved salts passes into the root-hair, but the primordial utricle acting as a semi-permeable membrane prevents the outward diffusion of many of the substances dissolved in the cell-sap

The presence of free oxygen and a suitable temperature are essential conditions of root-absorption Root-absorption increases with rise of temperature From what has been said it will also be understood that the presence of salts in large amount in soil water hinders absorption by the root, this is exactly what the root has to endure in salt marshes and peat-bogs

Exp. 12.—Place some dry raisins in water and observe that they swell up just as dry seeds do On the other hand, fresh grapes placed in a strong solution of sugar shrink. Both effects are due to osmosis

Exp. 13—Cover the mouth of a thistle-funnel with parchment or pig's bladder, and tie it on tightly Invert the funnel, and with a pipette add sugar solution till it reaches a short distance in the tube of the funnel Mark the level with a strip of gummed paper; then pass the tube of the funnel through a hole in a cork and support the cork so that the head of the funnel dips into a dish of distilled water Observe the rise of the liquid in the tube of the funnel; also show that a little of the sugar solution diffuses into the water, by evaporating the liquid in the dish to dryness, when a small residue of sugar will remain. If the sugar solution used is strong enough, the presence of sugar in the water outside the thistle-funnel may be detected by tasting.

Some idea of osmotic pressure may be obtained by using apparatus fitted up on the same lines as that shown in Fig 105, the pressure being measured by the rise of the mercury in the bent tube.

Exp. 14.—Cut sections of a piece of fresh beetroot; mount sections separately in (1) water, (2) salt solution, 3 to 5 per cent.; (3) alcohol. In (1) notice the layer of protoplasm ("primordial utricle") lining the cell-wall, and the red sap filling the cavity (vacuole) of the cell; some of the cells will be cut open, allowing the sap to escape. In (2) notice that the primordial utricle contracts from the cell-wall, but still contains the red sap. The salt solution can pass through the cell-wall, and, having a greater attraction for water than the osmotically active substances in the cell sap, withdraws water from the vacuole. The protoplasm allows water to escape, but not the osmotically active substances. This condition is known as **plasmolysis**. The cells can be restored to the normal condition by adding water. In (3) notice that the red sap diffuses out of the cells, which have been *killed* by the alcohol.

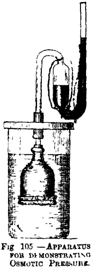


Fig 105.—APPARATUS FOR DEMONSTRATING OSMOTIC PRESSURE.

Exp 15.—Make a rough model of a root-hair out of a long potato-tuber. Cut off one end of the tuber so that it will stand upright, and with a knife scoop out the middle part, leaving on the outside a layer about a quarter of an inch thick. Half fill the tuber with salt solution or sugar solution (about 5 per cent. in each case), coloured with red ink, and stand it in a dish of water, the level of which should not exceed that of the salt or sugar solution inside the tuber. From day to day observe the rise of the coloured solution, showing that water has been absorbed from outside.

§ 6. **Chemical Processes in the Soil.**—Only substances in solution can be absorbed by the root-hairs. Substances insoluble in pure water and required by plants are brought into solution by various chemical processes which take place in the soil. Thus water containing carbon dioxide, which is always present in the soil, and is given out by the roots in respiration, can dissolve carbonate of lime and various silicates, and various soluble substances present in soil-water, by effecting

chemical decomposition, also bring insoluble substances into soluble forms.

Soluble salts are largely washed out of the soil by drainage The chlorides, sulphates, and carbonates are mostly removed in this way, but the soil, especially a clay soil, keeps a firm hold of potassium and ammonium salts, and also of phosphates, as can be shown by allowing dilute solutions to filter through samples of soil (see Exp 11)

Important changes take place in the organic matter of the soil The carbon in the organic matter is continually undergoing oxidation, carbon dioxide and organic acids being produced and heat given off, while, under the action of various moulds and bacteria, the nitrogen of the proteid substance is converted into ammonia, which largely unites with the carbon dioxide, forming carbonate of ammonia The carbonate of ammonia is oxidised, first into nitrites, and finally into nitrates; in this process, which is called **nitrification,** at least two distinct bacteria (nitrifying organisms) are concerned. Ammonium salts directly supplied to green plants are similarly converted into nitrates before they are absorbed.

Recent research seems to indicate that there are also in the soil various bacteria which have the power of making use of the free nitrogen of the air and bringing it into combined form, probably nitrates.

Exp. 16—Grow seedlings with their roots resting on blue litmus paper, or dipping into blue litmus solution, and notice the change of colour due to the excretion of carbon dioxide by the roots and root-hairs

Exp 17.—Grow seedlings in a layer of sawdust or soil resting on a slab of polished marble After a week or two remove the latter and examine its surface carefully for the tracks eaten into it by the roots

§ 7 **Selective Absorption by Roots.**—Different plants growing in the same soil absorb dissolved substances in very different proportions This has been determined by numerous analyses of the ash of plants, and it can also be proved by water-culture experiments This apparent selective power of plants is due to the fact that different

plants have different needs. Any diffusible substance in solution can be absorbed by the root-hairs, but its continued absorption depends on its being assimilated, or entering into the processes of metabolism. Cereals (Wheat, Rye, etc.) take from the soil less than half as much nitrogen, lime, and potash as "root-crops" (Turnip, Beet, Potato), but much more silica. The "rotation of crops" in farming is based on this. In this way, before any crop is grown again on the same ground, the special substances required by the crop have time to accumulate.

§ 8 **Course of Absorbed Solutions.**—The absorbed solutions pass *by osmosis* from the root-hairs into the cells of the cortical tissue of the root. Owing to the excess of endosmosis and the part played by the primordial utricle, a considerable pressure is set up in the cortical tissue—the cortical cells become extremely turgid. The solutions to a certain extent diffuse by osmosis through the parenchymatous tissue of the plant, but the greater part passes into the xylem tissue of the root, and is given off to the parenchyma at a higher level.

The passage into the xylem tissue is not effected by a process of osmosis, for at first the xylem elements (vessels) are empty, so that an essential condition of osmosis is wanting. It is brought about simply by the hydrostatic pressure set up as explained in the surrounding cortical tissue. It is probable that, when the limit of turgidity is reached (*i.e.* when the pressure exceeds a certain point), a molecular change takes place in the protoplasm (primordial utricle), and the watery solutions are expelled, owing to the collapse of the cell, with considerable force. In this way the solutions, following the course of least resistance, are forced into the wood vessels. They pass up through the xylem of root and stem, and out into the xylem of the leaf-veins. There they finally diffuse into the mesophyll tissue of the leaf, where elaboration chiefly takes place.

Formerly it was thought that the solutions passed upwards through the *walls* only of the wood elements, it is now known that they also pass through the cavities, and at certain periods the vessels contain abundance of

water. The water probably forms short columns with intervening bubbles of air, the columns, however, being connected by films along the wall of the vessel.

The current of water with dissolved salts passing upwards from root to leaves is called the **transpiration current.** It conveys food-materials to the leaves for elaboration, and makes good the loss of water due to transpiration.

Exp. 18—Fix a seedling with its root dipping into red ink (colouring-matter in *solution*), and after a time (try several seedlings, and give them different lengths of time) cut across the root, to see how far upwards the colour has spread, and in what part of the root it travels Also cut across the *stems* of seedlings that have been in red ink for a day or two, and notice the red-stained bundles how does the liquid travel in the *leaves*?

Exp. 19—Get any leaves with broad, thin blades and fairly long stalks—*e g* Radish or *Vinca rosea* (*alba*) Place them in bottles of red ink, with the cut lower end of the stalk dipping into the ink, and note the colouration of the veins Cut a Grass shoot above the creeping stem, and try the same experiment, noticing the arrangement of the veins, as indicated by the red lines which appear in the leaves in a day or two.

§ 9. **Root Pressure.**—We have explained that, owing to the great excess of endosmosis, a considerable pressure is set up in the cells of the cortical parenchyma of the root, that this is increased by the action of the primordial utricle, and that when the cells collapse the water is forced into the wood elements After collapse the cells recover their condition of turgidity and again collapse. In this way we can imagine that a rhythmical pumping of water into the wood elements is going on

Now this pressure which exists in the root, and which we may regard as a force driving the water into the wood elements, and upwards, is called **root-pressure.** In some plants it is very marked, especially in spring Thus, if the stem of a vigorous young Vine be cut in spring about a foot from the ground, there is an abundant exudation of watery sap from the vessels at the cut surface. This phenomenon is called "*bleeding*," and its manifestation continues for a considerable time Root-pressure can, however, be demonstrated in most plants, under suitable conditions, while active growth is going on, and there is sufficient water in the soil.

Depending, as it does, on root-absorption, root-pressure is affected by various external conditions, such as temperature, etc, which influence that process But it does not follow that, when root-absorption is active, there will be a high root-pressure, for the magnitude of the pressure depends also on the amount of transpiration. As a matter of fact, during a hot day, when transpiration is active, the amount of water absorbed by the root is usually not sufficient to make good the loss from the transpiring surface, and there is not merely no pressure in the vessels, but even a *negative* pressure, *i.e.* if the stem of the plant were cut across, the stump would absorb water applied to the cut surface instead of giving it out

On the other hand, after a very hot day, root-absorption continues active during the night, owing to the temperature of the soil, while transpiration is much reduced Under these conditions root-pressure may be sufficient to force drops of water out of the leaves, and thus get rid of the excess absorbed. This is the explanation of the drops of water seen in the early morning on the leaves of Saxifrages, Grasses, Garden Nasturtium, *Colocasia* (Kachálú), and other plants (see hydathodes, pp 54, 61). The water escapes through ordinary stomata, through water-stomata, or through the epidermis A similar exudation of water may be artificially induced by forcing water under pressure into a leafy branch.

Exp. 20.—Cut off the stem of a vigorous Bean seedling close to the ground, and connect the stump, by means of rubber tubing, to a long, straight piece of glass tubing; lash this tube to a stick placed in the soil, pour a little water into it, then a drop of oil, which will float on the water and prevent evaporation. Measure the ascent of the water in the tube, and find how the rate is affected by temperature.

Exp 21.—To measure the force exerted in root-pressure, an apparatus like that shown in Fig 106 may be used. *S* is a doubly bent (S-shaped) glass tube attached by rubber tubing to the cut stem; it is filled with mercury to the level *ss*, and there is water between the mercury and the stem. Root-pressure forces water into the tube and displaces the mercury to the levels *rr*. The force of root-pressure is measured by the difference of level.

Exp. 22.—Fix a branch of *Tropæolum* or a leaf of *Colocasia* in the short limb of a U-tube (containing water), as shown in Fig 106, and make the connection air-tight by means of rubber tubing By pouring mercury (Hg) into the long arm of the tube the water in the

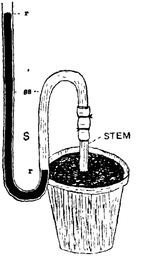


Fig 106 —APPARATUS FOR MEASURING ROOT PRESSURE (See text.)

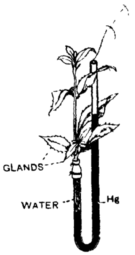


Fig 107 —MODE OF DEMONSTRATING THE EXCRETION OF FLUID WATER FROM LEAVES

short arm is forced under pressure into the stem and exudes in drops from the glands on the leaves The apparatus should be covered with a bell-jar over water.

§ 10 **Transpiration.**—A large amount of the water absorbed by the roots, and carried to the aerial parts by the transpiration-current, is given off from the aerial surface in the form of *water-vapour* This process is known as **transpiration.** The water vapour collects in the intercellular spaces of the parenchymatous ground-tissue, and passes off through the epidermis, and especially through the stomata Very little is given off from the general epidermal surface if the cuticle is at all well developed.

The process, however, is not simply one of evaporation. It is regulated by the vital activity of the plant. That this is so is evident from the fact that usually more water is evaporated from the surface of a dead leaf than from that of a living leaf. We must remember also that the stomata can regulate the amount of transpiration (see p 59).

Transpiration varies according to external conditions. It is more active when the air is dry and hot than when it is moist and cold This is not merely due to the fact that a hot dry atmosphere is favourable to evaporation, but also because it increases root-absorption.

Transpiration is greater in bright sunlight, because the latter increases assimilation and promotes osmotic activity. There is a rush of water to the assimilating cells. With this is correlated the opening of the stomata The guard-cells always contain chloroplasts, and we now have an explanation of this. The guard-cells become turgid when there is increased assimilation, owing to osmotic activity *When the guard-cells become turgid, the stoma opens;* when they collapse, it closes. The reason of this is found in the peculiar arrangement of thickening on the walls of the guard-cells (p 58). The thickening is such that the cells can expand only in a particular direction When turgid they bulge away from each other, becoming more convex on the side away from the pore, *concave*, or less convex, towards the pore

The stomata close if transpiration is too active, or if there is a deficient supply of water, they open in moist air, and other conditions where increased transpiration would be beneficial.

In transpiration plants get rid of the excess of water absorbed by the roots. Transpiration also acts as a force tending to cause the ascent of water from the roots to the leaves Further, it is probable that transpiration discharges an important function by keeping plants cool, more especially those exposed to direct sunlight.

Exp. 23.—Observe that a leaf plucked from a plant soon becomes dry and withered, and that whenever plants are grown under a bell-jar water collects on the glass.

Exp. 24.—Get a branch of *Citrus* in which the young leaves have become fully expanded, and attach it by means of a piece of stout indiarubber tubing to a glass tube about 9 ins long, with the end farthest from the branch bent at right angles for about 2 ins. Arrange the branch vertically, the longer limb of the glass tube horizontally, and the short terminal part dipping into water tinged with red ink It is best to cut the branch and attach the tubing under water in a large basin, so as to prevent the entrance into the stem of air-bubbles, which would diminish the flow of water

Notice that the coloured water soon begins to travel along the horizontal tube. This apparatus may be used to roughly measure the rate of the transpiration current. Ascertain whether the flow is different on bright and on dull days, and whether it is influenced by opening door and window so as to cause a draught What is the effect of smearing the surfaces of the leaves with vaseline? On different branches, smear (1) the upper surfaces, (2) the lower surfaces, (3) both surfaces, of the leaves, and note the rate of the transpiration current in each case.

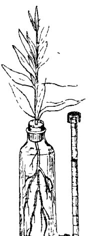


Fig 108 — APPARATUS FOR ESTIMATING THE ABSORPTION OF WATER BY THE ROOTS, AND THE LOSS BY EVAPORATION FROM THE LEAVES

Exp 25.—By the aid of a simple piece of apparatus (Fig 108) and a weighing balance, the amount of water lost by a leafy stem can be determined, and at the same time it can be proved that the amount transpired is approximately the same as that absorbed by the roots A plant is fixed by means of an air-tight indiarubber cork in a bottle filled with water. As water evaporates from the leaves and is absorbed by the roots, the level of the water in the graduated tube falls This gives the amount absorbed by the roots, and on weighing the apparatus it will be found to correspond to the total amount lost by evaporation from the leaves and stem. Each of the larger divisions on the graduated tube corresponds to a cubic centimetre of water, so that when the roots have absorbed that amount the entire apparatus will have lost about 1 gramme in weight

Exp. 26.—Get a plant growing in a flower-pot; any plant with thin (not leathery) leaves will answer. Cover the soil with an indiarubber sheet to prevent evaporation, and balance the pot on a pair of scales. Observe the loss of weight by transpiration Water

the soil daily or every two days, replacing the indiarubber sheet each time, and ascertain whether the loss of weight differs on bright and on dull days, in light and in darkness.

Exp. 27.—Cut three healthy leaves of Indiarubber Plant or of Rhododendron. Attach a small piece of fine rubber tubing to the stalk of each; fold the rubber back and tie it tightly to prevent evaporation. Cover the lower surface of one leaf (A), and the upper surface of the second (B), with vaseline; leave the third (C) untouched. Tie a piece of wire or string to each leaf, and weigh them carefully. Hang them up near each other and weigh them each day. After several days the leaf whose stomata are blocked (A) will be still green and fresh, while the others will be more or less withered.

Exp. 28.—Soak some filter papers in a 5 per cent solution of cobalt chloride. Dry them and observe that they turn blue. Breathe on one of them and notice the change of colour. These cobalt papers afford a delicate test for water-vapour. Place a thin leaf between two of them, and keep them flat by placing them between two pieces of glass. Notice which surface of the leaf gives off most water vapour, as shown by the change of colour.

Exp. 29.—Strip off a piece of the lower epidermis of a leaf of Bean or Narcissus, mount in water and examine with the microscope. Find an open stoma with the high power; put a drop of 3 per cent salt solution at one side of the cover glass and draw it through with blotting-paper. The salt solution draws water out of the guard-cells and the stoma closes. If water is now drawn through in the same way, the guard-cells absorb it and swell up, and the stoma opens.

§ 11. **Causes of the Ascent of Water.**—The elucidation of the causes of the ascent of water in tall trees in opposition to the action of gravity has been, and still is, one of the problems of botanical physiology. It cannot even yet be said that they have been definitely or fully determined.

The first theories were vitalistic, vaguely ascribing the ascent to the vital activity of the living protoplasmic substance. These, by themselves, were little more than a confession of ignorance. Various physical causes have since then come under discussion, such as root-pressure, transpiration, capillarity in the wood-vessels, the varying pressure of the gases contained in the wood-elements, and so on.

The importance of most of these has been discounted for physical and other reasons. Thus it has been shown, in the case of root-pressure (p. 167), that when transpiration is active there may be a negative pressure in the wood-vessels, and that poisonous solutions, i.e. solutions which would kill the living protoplasm, can be absorbed and *ascend* through the xylem, although, as has been explained, the

vital activity of the protoplasm probably plays an important part in connection with root-pressure. Transpiration, however, is generally regarded as a factor having an important influence on the ascent of water. It causes a great diminution of pressure in the upper parts of trees, and the pressure is equalised by the upward passage of water from the lower parts. Thus transpiration might be loosely regarded as a force sucking up the water from below.

Exp. 30.—The sucking force exerted by the leaves can be demonstrated by attaching a leafy branch, cut under water, to a tube filled with water and dipping into a coloured solution. It will be found that the solution ascends the tube even when the latter is many feet in length.

§ 12 **Photosynthesis (Carbon-Assimilation).**—Carbon dioxide is absorbed by the plant over its green aerial surface—chiefly the leaves—in the presence of light. It passes into the intercellular spaces by means of the stomata and diffuses from the intercellular spaces into the parenchymatous cells—the mesophyll cells in the case of leaves. It should be noticed that it passes through the walls, not as a gas, but in solution. It is dissolved in the cell-sap which permeates the walls of the cells. In the interior of these cells chemical processes, leading to the elaboration of organic compounds, take place.

This elaboration, of the details of which little is known with certainty, goes on chiefly in the mesophyll cells of foliage leaves, although also to some extent in green herbaceous stems. Under the influence of chlorophyll and light the water (H_2O) absorbed by the root and the carbon dioxide (CO_2) are built up into carbohydrates. The first compound formed is probably **formic aldehyde** (CH_2O), and oxygen (O_2) is given off in the process. This may be represented according to the equation—

$$CO_2 + H_2O = CH_2O + O_2,$$

although it is very doubtful if this can be regarded as a true representation.

It has been suggested that there may be an intermediate step, thus —

$$\begin{aligned} CO_2 + H_2O &= (CO + O) + (H_2 + O) \\ &= CH_2O + O_2 \end{aligned}$$

There seems, however, to be very little evidence in support of this From the formic aldehyde soluble carbohydrates of the nature of sugars may be formed by a process of compounding (polymerisation). Thus we may imagine the formation of grape-sugar ($C_6H_{12}O_6$) —

$$6CH_2O = C_6H_{12}O_6.$$

Some recent chemical experiments, however, seem to show that, in many plants, cane-sugar ($C_{12}H_{22}O_{11}$) is the first sugar formed

Thus, in carbon-assimilation, carbon dioxide is taken into the plant and, along with water, undergoes a chemical change, an equivalent volume of oxygen, approximately, is given off, and the carbon made use of in the elaboration of organic substances of the nature of carbohydrates.

The surplus amount of sugar formed in the leaves is stored up as starch in the chloroplasts (p 33) The rest is transferred from the seat of formation to other parts of the plant and made use of in ways to be described presently

Formerly it was thought that the starch appearing in the chloroplasts was *directly* built up from carbon dioxide and water, *i e* that the carbohydrate starch was the first carbohydrate formed in the process We may still regard starch as the first *visible* product giving evidence of carbon-assimilation: but we can no longer regard it as being formed directly It is simply a temporary *storage* of surplus carbohydrate. During the night it is reconverted into sugar and passes out of the leaf (see p 187)

In many green plants, especially Monocotyledons (*e g* the Onion), no starch is formed in the chloroplasts, or even in more permanent store-places of food-material. In the cells of these plants various forms of sugar take the place of starch. It may be mentioned here also that in many Algæ, e g *Vaucheria*, the products of assimilation are not carbohydrates, but various forms of oil.

Exp 31.—Boil in water some leaves taken from a Bean seedling, or some other plant with thin flat leaves. The colour does not come out Place the boiled leaves in alcohol, and notice that the leaves gradually lose their colour, while the alcohol turns green.

When the leaves are colourless, place one of them in a saucer and pour dilute iodine solution over it. The depth of colour produced shows roughly how much starch is present. If there is abundance of starch, the colour is nearly black; if little starch, it is bluish; if none, the iodine turns the leaf brownish (test for proteids). If the leaves of a plant growing in the light are tested in this way there will be abundance of starch; there will be none if the plant has been kept in darkness for one or two days.

Exp. 32.—To show that the presence of chlorophyll is necessary for carbon assimilation and starch formation in leaves apply the iodine test to some variegated leaves (*e.g.* varieties of cultivated *Coleus*). Observe that only the green parts produce starch. It is advisable to make a careful drawing of the leaf before applying the test. Further, it can be observed that in leaves whose veins are colourless, or nearly so (*e.g.* *Fittonia*), owing to the absence of chlorophyll above and below them, the veins stand out from the rest of the leaf, when the iodine-test is applied, by the absence of starch.

Exp. 33.—Put a seedling, which has been kept for two days in darkness, into a small bottle containing water, so that its roots only are in the water. Pour some caustic potash into a wide-necked glass jar, and lower the bottle with the seedling into this jar. Cork the jar tightly and smear the edges of the cork with vaseline; but pass the tube of a funnel containing soda-lime through a hole in the cork. The seedling is thus supplied with air, but all the carbon dioxide is absorbed by the potash solution and the soda-lime. If the leaves be tested after sufficient exposure to light they will be found to contain no starch. A control experiment should be set up in which the arrangements are the same, except that the potash solution is omitted and gravel is placed in the funnel instead of soda lime.

Exp. 34.—Pin to the leaf of a plant, which has been kept in darkness for at least a whole day, two flat slices of cork opposite each other on the two sides. Smear a small circular area of another leaf with vaseline, applying it to both sides. Expose the plant to light from morning till late afternoon. Then remove the leaves and apply the iodine test. No starch will be found in the parts protected from light or whose stomata have been blocked by vaseline.

Exp. 35.—Tie the leaves of some ordinary land plants to a stone and sink them under water in a glass jar. After sufficient exposure to light test the leaves, no starch will be found. If the experiment is repeated with the leaves of a water-plant—e.g. *Hydrilla*, *Myriophyllum*, or *Utricularia*—it will be found that abundant starch is found. Why?

Exp. 36.—Place some water plants, e.g *Hydrilla*, *Myriophyllum*, or American Water-weed, in a large glass vessel exposed to bright light, and observe the bubbles of gas given off. Cover the vessel with a black cloth so as to cut off the light, and observe that the bubbling stops after a time. Press a glass funnel down on the plants, when they are again exposed to light, and invert over it a test-tube filled with water, so as to collect the gas given off. That the gas is chiefly oxygen is easily proved by its causing a glowing splinter of wood to burst into flame No gas is given off, and there is no formation of starch, if the water has been boiled, because in this case the water contains no carbon dioxide.

§ 13. **Conditions of Carbon-Assimilation.**—It is evident there must be a supply of water and carbon dioxide Heat, also, is necessary; this is a general condition of plant-metabolism Metabolism and growth can take place only within certain limits of temperature Heat is a source of energy and a necessary condition for the initiation and continuation of all vital processes in plants. The more special factors in carbon-assimilation are light and the presence of chlorophyll We have now to consider more fully the part played by these

§ 14 **Light.**—In our laboratories we can effect the decomposition of carbon dioxide and of water only by the expenditure of a large amount of energy—heat energy in the former case, electrical energy in the latter The building up of complex substances containing a very small proportion of oxygen also means expenditure of energy The green plant carries on both these processes at ordinary temperatures Light being an essential factor, we come to the conclusion that it is so because it is the chief source of energy. The energy used is stored up in potential form in these compounds

When a beam of sunlight is passed through a prism it is spread out into a band, called the spectrum (which can be received on a screen), consisting of many different colours, passing gradually from one to the other. This is because sunlight consists of many different kinds of rays differing in refrangibility, *i e* as regards the angle through which they are bent on passing through a prism At one end of the spectrum are *red* rays, which gradually pass

through *orange and yellow*, to *blue and violet* rays at the other end Now all these rays are not equally active in the process of carbon-assimilation It has been determined, by direct experiment, that the red rays are the rays chiefly concerned in the process.*

Exp. 37.—Obtain a pair of double-walled bell-jars. Fill the space between the walls of one of them with a watery solution of potassium dichromate, and that of the other with a watery solution of copper sulphate, to which ammonia has been added. The first solution allows red rays to pass through, the second one blue rays. Set each bell-jar on a folded cloth, or in a saucer of dry sawdust, so as to shut out any white light Place under each a plant in a pot or a seedling that has been dug out and had its root set in a bottle of water Set both bell-jars in diffused light; in direct sunlight the temperatures in the two would not be the same. The plant in the red orange light will be found after exposure to light (let the experiment last for two days) to have formed abundant starch; that in the blue light will be almost free from starch.

Exp. 38.—Watch the bubbles of oxygen arising from a submerged water-plant (see Exp. 36), and time the rate of bubbling When this is fairly regular, cover with the blue bell jar, and notice that the bubbling becomes slower after a short time. After about five minutes (take several readings during this time) take off the blue jar and put on the red orange one, taking records of the rate of bubbling as before, noting the increase in red as compared with blue light.

§ 15. **Chlorophyll.**—The green colouring matter of plants is a complex substance consisting of carbon, oxygen, hydrogen, nitrogen, and magnesium. It is really a mixture of two components, a blue-green pigment called chlorophyll-*a* ($C_{55}H_{72}O_5N_4Mg$) and a very similar yellow-green pigment called chlorophyll-*b* ($C_{55}H_{70}O_6N_4Mg$) Associated with the chlorophyll in the chloroplasts are two other colouring matters, orange-red *carotin* ($C_{40}H_{56}$—a hydrocarbon) and yellow *xanthophyll* ($C_{40}H_{56}O_2$—apparently an oxidation product of carotin) Only chlorophyll is concerned in photosynthesis Chlorophyll is readily decomposed by bright light in the presence of oxygen

Two conditions, in addition to oxygen and a suitable temperature, are necessary for the *formation* or development of

* Plants may be grown under artificial light, *e g* electric.

chlorophyll.—(*a*) the presence of light,* (*b*) a supply of iron in the food.

If a plant is grown in darkness, it assumes a pale yellowish sickly appearance. This is due to the fact that a yellow colouring matter—**etiolin**—is developed in the corpuscles instead of chlorophyll. Such a plant is said to be *etiolated*. Of course, a plant grown in darkness must have some reserve store of food-material to draw upon, as, for example, a potato-tuber developing in darkness. Many examples of etiolated plants will readily occur to the mind of the student, *e.g.* Celery, grass covered by a roller or a board.

Typical etiolated plants present many other peculiarities. Thus the internodes become very much elongated or "drawn out." For this reason the plants are called **"drawn plants."** This has an important biological significance. In this way there is a chance of shoots reaching the light, as, for example, in seedlings smothered by other plants. In etiolated plants, also, the leaves remain small and scaly, there is an enormous development of soft succulent parenchyma and a meagre formation of lignified tissue. Large leaves would be useless in darkness; we might say, therefore, that the plant devotes all its energy to the formation of long internodes which may be of use to it.

It has been determined by experiment that the action of light in promoting the formation of chlorophyll is due not only to the red rays, but also to the blue and violet rays.

A yellowish, sickly condition is also established if there is no iron in the food, the plastids being colourless or containing etiolin. This condition, due to the want of iron, is called the **chlorotic** condition. It is to be carefully distinguished from the etiolated condition due to the absence of light. As soon as the plant is supplied with a *weak* solution of an iron salt, even if it is only applied to the leaves, chlorophyll is developed. Thus iron is necessary to the formation of chlorophyll, although it does not enter into its composition.

* In exceptional cases chlorophyll is developed in darkness (cotyledons of Ferns and of a few seeds—*e.g.* Sycamore, *Pinus*).

Chlorophyll can be extracted by means of alcohol, chloroform, etc. If green leaves are boiled in water, and then placed in alcohol, a solution of chlorophyll is readily obtained. A solution of chlorophyll is fluorescent—it is green by transmitted light, red by reflected light.

When a solution of chlorophyll is placed in the path of a beam of light, which is then passed through a prism, the spectrum is modified. Certain dark bands (absorption-bands) appear in the spectrum, more especially in the red region. This is because these particular rays have been absorbed by the chlorophyll. This leads us to the function discharged by chlorophyll. We have seen that the red rays are especially active in carbon-assimilation. We therefore conclude that chlorophyll is a colouring matter which, by absorbing certain rays of light, supplies the living protoplasm with the energy necessary for carrying on the chemical processes connected with carbon-assimilation. It may be that the radiant energy is by the chlorophyll-apparatus converted into electric energy.

Exp. 39.—Grow seedlings, *e.g.* Cress or Mustard, in darkness, then place some of them in a good light, close to a window, and note the time required for the production of a distinct green colour. Place the others in a dark part of the room, and when they have become green test the leaves for starch. These observations will show that (*a*) a green tinge, due to formation of chlorophyll, may be developed in an hour or less, in good light; (*b*) light too weak for photosynthesis is strong enough for the production of chlorophyll.

Exp. 40.—Place some etiolated seedlings (Cress, Mustard, Bean, etc.) in a bottle or small glass jar, cover with a glass plate, and set it in a larger jar half filled with water. Keep the water at 30° C. In a similar apparatus keep some of the seedlings in cool water, or water kept at 10° C., by adding bits of ice from time to time. Compare the depth of the green colour developed in the two sets of seedlings after an hour or two.

Exp. 41.—Fill a test-tube with water, invert it in water, and pass under its rim some etiolated Mustard seedlings. Though exposed to light the seedlings do not become green, owing to lack of oxygen.

Exp. 42.—Extract chlorophyll from green leaves by boiling them in water, draining off the water, and covering the leaves with alcohol. Then place the dish containing the leaves and alcohol

in the dark; light destroys the colouring matter in the solution. Filter the solution, and place it in a corked bottle. Notice the colour of the filtered extract by holding the bottle up to the light, and by holding it against a black surface. Obtain a continuous spectrum on a screen by fastening on the lens of an optical lantern a card with a vertical slit, and holding a prism in the path of the light. Hold a test-tube of chlorophyll-solution against the slit, and notice that the colours in several parts of the spectrum are replaced by dark bands. The most prominent dark band appears in the red part, but if the solution is strong enough other bands will be seen in the green and blue.

Exp. 43.—Fill three test-tubes with chlorophyll extract, cork them, and place A in sunlight, B in diffused light, C in darkness. Carefully boil some extract in a fourth test-tube D, and place it with A in sunlight. Notice, after a day's exposure, that A becomes brown, C is unchanged, while B and D are only slightly changed; the absence of oxygen in D hinders the destructive effect of light.

§ 16. **Formation of Nitrogenous Substance.**—The elaboration of nitrogenous substance is not so clearly understood as that of carbohydrates. Various complex soluble nitrogenous substances of the nature of amides (*e.g.* asparagin, $C_4H_8N_2O_3$) are apparently formed. The simplest process leading to the formation of amides would be the interaction of sugar and nitrate of potash, the chief products being asparagin, which is widely distributed in plants, and oxalate of potash. The latter, like oxalic acid itself, is poisonous, but it reacts with the calcium salts brought up from the soil, forming oxalate of lime, which, being insoluble in water, crystallises out and is rendered harmless. This is probably one source of the oxalate of lime which occurs so abundantly in crystals in plant-tissues. These crystals are more abundant in leaves exposed to full sunlight than in shaded leaves, and in the green than in the not-green parts of variegated leaves.

Nitrate disappears from cut leaves in a few days if they are exposed to light; in variegated leaves the nitrate disappears only from the green parts. Thus the disappearance of nitrate from leaves is related in the same way to light and chlorophyll as is the accumulation of calcium oxalate.

However the elaboration of amides be effected, there is no doubt that they are, sooner or later, produced as the result of synthetic processes There is some evidence, such as that indicated above, to show that light is necessary as a source of energy, and that the process also depends in some way, directly or indirectly, on the presence of chlorophyll. Inasmuch as the previous formation of carbohydrates may be a necessary condition for the assimilation of nitrogen the influence of chlorophyll on the process may be only indirect The further elaboration of amides into proteids (§ 17) appears to be related in the same way to the presence of light and chlorophyll.

Exp. 44.—Place young and old leaves of species of Aroids, etc, in strong solution of chloral hydrate, which makes them transparent, and examine with the microscope Notice the abundance of oxalate crystals in old as compared with young leaves, in leaves growing in full sunlight as compared with leaves from the shaded part of the tree, in the green as compared with the non-green parts of variegated leaves

Exp. 45.—The presence of nitrates in a leaf can be detected by cutting rather thick sections of the blade or the stalk, placing them on a glass slide, and adding a drop of diphenylamine sulphate if nitrates are present, a deep blue colour appears Cut off the leaves of various plants and test them in this way, if they give the blue colour, set other leaves in the light with their stalks in water, and after a few days test again for nitrates Test in the same way (1) the leaves of plants exposed to bright light, and compare with leaves of plants of the same species kept in deep shade, (2) variegated leaves of a plant exposed to bright light

§ 17. **Transference and Destiny of the Elaborated Compounds.**—Thus we have explained, as far as possible, the building-up of soluble carbohydrates (sugars) and soluble nitrogenous compounds (amides) in the assimilating cells—chiefly the mesophyll cells of leaves. With the exception of what is made use of in the assimilating cells, the sugars and amides are transferred to the various parts of the plant *All* living cells contain these soluble carbohydrates and nitrogenous compounds conveyed to them in the cell-sap The living protoplasm makes use of these as food substance Together with sulphur and phosphorus derived from sulphates and phosphates, they

are built up first of all into proteid substances, and, finally, into protoplasm. This final elaboration is most active where rapid growth is taking place, *i.e.* at growing points.

Many of the soluble compounds, however, are made use of in the formation of insoluble storage compounds. The formation of starch in the chloroplasts, to which we have already referred, is only one example of this. Storage products may be formed in any living cell, but the formation is specially abundant in particular tissues or organs, *e.g.* medullary rays of trees, seeds, bulbs, corms, rhizomes, etc. The formation and uses of these products are explained in §§ 21 and 23.

In the process of transference from the assimilating cells, the sugars and amides may, to a certain extent, pass from cell to cell by simple diffusion. But a more rapid transference is effected through the phloem-tissue. In this way they are quickly conveyed to regions where rapid growth is going on, or where a storage of food-material is taking place.

Formerly it was thought this rapid transference was effected through the sieve-tubes only. It is now certain that the phloem-parenchyma (and the neighbouring parenchyma of the ground-tissue) is chiefly concerned in the transference of the carbohydrate material. This also *may* apply to the nitrogenous substance. According to some, there is a formation of proteid or albuminous substance in the phloem-tissue, and they regard the sieve-tubes as being temporary store-places of these products. We have seen that the sieve-tubes do contain such substance.

One of the chief forms in which sulphur enters the plant is calcium sulphate. The sulphur is liberated, and thus enabled to combine with the organic food substance, by the action of an organic acid. This acid appears in many cases to be oxalic acid. The calcium of the sulphate combines with the oxalic acid to form calcium oxalate.

Exp. 46.—Place a Bean seedling or a Garden Nasturtium (try various other plants) in darkness for a few days, then remove some leaves and test them for sugar by boiling them in Fehling's

solution.* There will be little or no red colouration, showing that sugar is absent or nearly so. Expose the plant to sunlight for several hours, then place it in darkness (after having tested some leaves, or parts of leaves, for starch), and after a time test some leaves for sugar, which will be indicated by the red colour produced around the veins. If the presence of sugar is detected in this way in the leaf-blade, test sections of the leaf-stalk at different levels, to find out by what paths the sugar travels towards the stem. Also test sections of the stem itself.

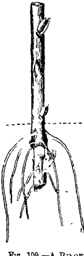


Fig. 109.—A Ringed Branch sprouting in Water.

Exp. 47.—Make two cuts round the lower part of a Willow twig, about an inch apart, and remove the soft outer tissue of the stem between these cuts, so as to leave only the hard woody portion of the stem for this distance. Then set the twig in water (which should be changed every day) or in culture-solution, and notice that it begins to sprout after a few days (Fig. 109). Below the injury the development of buds and new roots takes place but slowly, whereas above it new roots are rapidly formed.

This experiment usually succeeds best in spring or early summer. Later in the year it is advisable to remove the leaves in order to diminish the loss of water, since there are no roots on the cutting to keep up the supply of water. The rapid development of buds and the formation of roots above the ringed part show that food passes down chiefly through the soft outer region of the stem.

§ 18. **Use of the Metallic Elements, etc.**—So far, in connection with these processes of elaboration, we have had little occasion to mention the metallic elements of the food material. Potassium, calcium, magnesium, and iron do not enter to any extent into the composition of the living substance or of the cell-wall,† yet they are essential

* Fehling's test. Dissolve 35 grammes of copper sulphate in 200 c.c. of water to make solution A. To make solution B (to be kept in a separate bottle) dissolve 70 grammes of Rochelle salt in 200 c.c. of 10 per cent. caustic potash solution. Use equal volumes of solution A, solution B, and water.

† Calcium is present in the middle lamella (see p. 43), and iron apparently is present in nuclear substance.

elements (p 156). Now we have seen that iron, although it does not enter into the composition of chlorophyll, is necessary for its formation. This gives us a hint as to the use of the other elements. It would seem that potassium in the same way is a necessary condition for the formation of carbohydrates, and that calcium and magnesium are necessary for the proper distribution of carbohydrates. Calcium is also of importance in the formation of more complex substances from carbohydrates, since it combines with, and thus makes harmless, the poisonous by-product (oxalic acid) which is formed in these processes.

§ 19 **Katabolic Processes.**—We have hitherto been dealing with the anabolic processes of metabolism (p. 14), the processes by which simple compounds are *built up* into complex organic compounds. The final result of synthesis is the elaboration of living protoplasmic substance. We have now to consider the katabolic processes (p 14) in which the complex and unstable substance protoplasm undergoes decomposition and breaks down into simpler and more stable compounds. These processes are intimately associated with growth, and are as essential as the anabolic processes.

All growth takes place *from* and *in* the living substance protoplasm. While the anabolic processes are concerned with the nourishment and building up of living protoplasm, the katabolic processes lead to the formation of various substances which are absolutely necessary either for carrying on the anabolic processes or for building up the tissues, and at the same time set free energy which is expended largely in connection with growth.

As explained on p 14 the decomposition of the protoplasmic substance is a slow process of oxidation, and the substances produced are either plastic substances, secretions, or excretions. Oxygen passes into the plant in **respiration** and is absorbed by the protoplasm. As a result the protoplasm undergoes decomposition. These katabolic changes are stimulated or influenced in various ways by the action of external agencies, such as temperature, light, gravity, etc.

§ 20. **Respiration.**—In this process oxygen is absorbed by all parts of plants. There are no special respiratory organs in plants, but the absorption of oxygen is most rapid in the regions or organs where the katabolic processes are most active, *e.g.* leaves, growing points, germinating seeds. Carbon dioxide is given off as an almost invariable excreted product arising from the decomposition of protoplasmic substance. In aerial parts protected by a firm cuticle or a layer of cork, the oxygen enters by means of stomata or lenticels. It passes through the cell-walls into the interior of the cells in solution. The process of respiration is masked during the day, owing to the activity of carbon-assimilation.

The student must carefully distinguish between respiration and photosynthesis (carbon-assimilation). The following table indicates the chief points of distinction:—

Respiration.	**Photosynthesis.**
(*a*) A *breathing* process associated with katabolism.	(*a*) A *feeding* process associated with anabolism.
(*b*) Takes place over whole surface.	(*b*) Only in green aerial parts.
(*c*) O_2 passes in, CO_2 given off.	(*c*) CO_2 passes in, O_2 given off.
(*d*) Independent of light and chlorophyll.	(*d*) Dependent on light and chlorophyll.
(*e*) Plant loses weight.	(*e*) Plant gains in weight.

There is no constant relation between the volume of oxygen absorbed and the volume of carbon dioxide exhaled. The latter may be approximately equal to, less, or greater than the former. In a few succulent plants it has been observed that no carbon dioxide is given off at all, but that there is a marked increase in the organic acids present in the sap. In this case the process of decomposition is not so complete as in other cases, and has stopped short of the formation of carbon dioxide.

On the other hand carbon dioxide may be exhaled without any absorption of oxygen. This can be observed in the case of various seeds when made to germinate and deprived of oxygen. The necessary oxygen is apparently obtained not from outside, but by decomposition of complex compounds in the plant itself. This *intramolecular* or ***anaerobic***

respiration, as it is called, is not a normal process in ordinary green plants, which if deprived of oxygen soon die, but it is commonly met with in the Fungi and Bacteria, and is closely related to the process of fermentation

Exp. 48.—Place a bunch of roots, or some onions sliced in half, or twenty to thirty germinating peas, in a jar. After a day or two lower a lighted taper into the jar and observe that it is extinguished; or pour some lime-water into the jar and observe that it becomes milky These tests show that carbon dioxide has been produced in abundance This occurs whether the jar is exposed to light or not, for with the materials used there is no carbon-assimilation, and respiration is equally active under both conditions.

Exp 49.—Suspend three healthy Croton leaves by threads from the well-fitting cork of a large bottle containing lime-water, and expose them to bright light. After several hours the lime-water is still comparatively clear Cover the bottle with black cloth, and in a few hours the lime-water will become quite milky, owing to the respiration being no longer masked by the re-assimilation of the carbon dioxide it produces

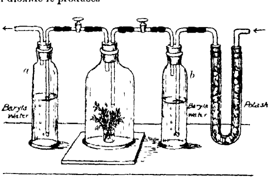


FIG 110 —THE ARROWS SHOW THE DIRECTION OF THE CURRENT OF AIR, WHICH IS DRAWN THROUGH BY ATTACHING AN "ASPIRATOR" AT THE LEFT OF THE APPARATUS

Exp. 50.—Place some green leaves in a glass jar (Fig. 110) through which a slow current of air is passed. This air is deprived of its carbon dioxide by the potash contained in the U-tube. The baryta-water in both (*a*) and (*b*) remains clear so long as the leaves are exposed to sunlight or very bright daylight, whereas if the glass jar is covered with a black cloth the liquid in (*a*) soon becomes turbid and milky.

Exp. 51.—To demonstrate intramolecular respiration soak six peas in water for a day or until the coats can be removed without damaging the embryo. Fill a test-tube with mercury and invert it in a dish of mercury; then pass the seeds under the open end of the tube, when they will float up to the closed end. In a day or so the test tube will be half full of gas. With a bent tube pass a little water under the test-tube, so that it will float up to the surface of the mercury, then pass up a small piece of caustic potash; the strong potash solution thus formed absorbs the gas. This shows that it is carbon dioxide.

Exp 52—Take about forty beans as nearly alike in size and weight as possible; select four of them as samples, and find their weight after thoroughly drying them on a water- or sand-bath or in a slow oven. Take the dry weight of a seed, found in this way, as the average. Sow half of the seeds in sawdust in a box which is kept in darkness, the other half in a box kept in full light; water both lots about equally. At the end of each week remove three seedlings from each box, wash the roots in running water (do not leave any in the sawdust or lose them in any way), and dry them thoroughly without charring any part. When quite dry and brittle, weigh each lot and obtain the average weight of the solid matter in each plant.

The results may be plotted on a sheet of squared-paper. As the weekly observations proceed trace two curves across the sheet, one in black ink to show the weight of the seedlings grown in light, the other in red ink to show the weight of those grown in darkness. The results will clearly demonstrate the loss of weight associated with respiration, and the increase of weight associated with carbon-assimilation. It will be found that the dry weight of the seedlings grown in darkness decreases, while that of those grown in light increases.

§ 21 **Plastic Substances.**—We have seen that some of these are formed anabolically, *e g* sugars, amides, proteids. The most important formed katabolically are cellulose, starch, oil, and very probably proteid grains (aleurone grains). Cellulose is formed in all cells where the cell-wall is undergoing extension or thickening. The others are storage food-substances—as also is cellulose in many seeds (*e g* Date).

We must now say something more with regard to the formation of starch. It was formerly thought that it was formed by a *direct* conversion of sugar effected by plastids, and that the process might be represented by the equation

$$C_6H_{12}O_6 - H_2O = C_6H_{10}O_5.$$

The view now generally adopted is that starch is not formed directly from sugar, but *indirectly* and *katabolically* The process is carried on by plastids, usually leucoplasts or chloroplasts The plastids, from the soluble carbohydrates, amides, etc, presented to them, *build up their protoplasmic substance.* The starch formed by the plastid is produced katabolically by the decomposition of the living substance of the plastid In the chloroplasts the storage of starch is temporary. The starch which is formed there during the day disappears at night In tubers, seeds, etc., the storage in connection with leucoplasts is more enduring.

Starch and cellulose are the chief forms in which carbohydrate is stored up In some plants, however, other forms of carbohydrate are found, *e g.* inulin (p 37), grape-sugar (in Carrot), cane-sugar (in Beet and Onion, p 173), the formation of these, also, may be katabolic. Aleurone grains (and proteid crystalloids) represent the chief storage of nitrogenous substance. As a storage product oil occurs in many seeds

Exp 53—Cut thin sections of the cotyledons of the Sunflower seed or of the endosperm of the Castor-oil seed. Examine these in water under the microscope, and observe the bright, highly refractive globules of oil. These can be dissolved by adding ether; those of the Castor-oil are soluble in alcohol Add potash solution to the sections and warm gently; the globules become cloudy (owing to saponification) and are finally dissolved.

Exp. 54.—Cut sections of Beet-root. Examine in water and observe the coloured cell-sap Soak the section for some time in alcohol, and examine again. Small crystals of cane-sugar will be observed. If to the coloured extract, formed by boiling pieces of Beet-root in water, Fehling's solution (p. 182, footnote) be added, and the liquid boiled, no precipitate of cuprous oxide is formed. Cane-sugar differs from grape-sugar in giving a precipitate only after prolonged boiling.

§ 22 **Secretions and Excretions.**—The most important secretions are colouring matters (chlorophyll, the colouring matter of flowers, etc), organic acids, ferments (see p 34) The chief excreted substances formed katabolically are carbon dioxide, resins and gums, tannin, alkaloids, etc. (p. 34). It should be noticed that, in plants,

there are no special excretory organs Still, many of these excreted substances are got rid of, e.g. in falling leaves, the scaling of bark, etc We find that the leaves of deciduous trees become filled with such substances towards the approach of winter So also the bark. Falling to the ground these substances are decomposed and brought into forms in which they may again be absorbed by plants.

§ 23 **Storage Material—Ferments.**—The various storage forms of food-material are, sooner or later, made use of First of all, however, they must be brought into a soluble diffusible form. This is effected by the action of certain soluble nitrogenous bodies of the nature of unorganised ferments or enzymes, which, as we have seen, are formed katabolically from the protoplasm. These ferments are substances which have the power of inducing important chemical changes without themselves being changed The changes are essentially similar in nature to those of digestion in animals. As a result the insoluble storage substances are converted into forms in which they can diffuse through the organism and serve as food to the protoplasm.

Many of these ferments have been extracted from plants, and there are doubtless many more which have not yet been extracted. There are two forms of diastase which act on starch and convert it into malt-sugar. *Maltase* is a ferment which converts malt-sugar into grape-sugar Other ferments, known as proteolytic ferments, act on proteids and convert them into soluble peptones, or reduce them to simpler forms (*e g.* amides) There is a ferment, *lipase*, which emulsifies fats and oils, and breaks them up into glycerine and fatty acids (p 40), which then undergo further alteration; from the glycerine sugar is formed, and part of this may be stored up as starch, which generally appears in the cells of the embryo of oily seeds during the process of digestion There are also ferments, *cytase*, *inulase*, *invertase*, acting respectively on cellulose, inulin, and cane-sugar

The soluble diffusible substances produced are often identical with the soluble substances formed anabolically

(sugars and amides), and are used in the same way by the protoplasm in building up its substance The action in most cases is one of hydration. This taking-up of water is accompanied by decomposition and liberation of energy, so that ferment-action comes under the head of katabolism.

Exp. 55.—Make thin starch-paste by shaking up a little ordinary starch or flour with boiling water and letting it stand to cool. Get some Pea seedlings in which the radicle has grown out at least an inch, remove the seed-coats, grind the cotyledons up with water, and filter through a funnel with filter-paper or thin blotting-paper. Pour the starch-paste into white saucers, putting a label on each Leave saucer 1 as it is; into 2 pour a few drops of iodine solution; into 3 pour some of the watery extract from the cotyledons. Set the three saucers in a fairly warm place, and after a time test 1 and 3 with iodine solution. Notice that the starch-paste with the extract in it soon gives only a reddish colour with iodine, and ultimately remains uncoloured by iodine, showing that the starch has disappeared. Taste the liquid in saucer 3, to which the extract was added, the starch has been converted into sugar by a substance (diastase) which has been extracted from the cotyledons.

Exp. 56—Squeeze the milky contents of about half a dozen sprouting Wheat-grains into a test-tube or watch glass with a little water, and stir. Filter, add a few drops of Fehling's solution to the clear filtrate, and heat. A brick-red colouration indicates the presence of sugar

Exp. 57.—Shake up some linseed oil with its own volume of 50 per cent. alcohol (diluted methylated spirit) and test it with litmus papers, it is neutral Add to the mixture some Castor-oil seeds which have just begun to germinate (crush or chop them up), and test again with litmus after a few hours; note the acid reaction due to fatty acids.

§ 24 **Energy.**—We have seen that energy is derived by the plant partly from heat, chiefly from light The energy absorbed is stored up in potential form in the complex organic substances formed In the katabolic processes there is a liberation of energy. The liberated energy is for the most part made use of again in building up the living substance of the plant, so that we may say that the greater part of the energy which enters the plant is accumulated in potential form in the complex substances formed.

But a certain amount of energy is dissipated or given off in various ways. A certain amount of energy in potential form is, for example, lost to the plant in the various complex excreted substances which are got rid of. When the katabolic processes are very active, as in the unfolding of many massive inflorescences, or the germination of large numbers of seeds, a dissipation of energy in the form of heat can be recognised, a distinct rise in temperature is noticed. Again, many plants show movements of various kinds, growth itself may be regarded as a slow form of movement. This also means a loss of energy to the plant.

Exp. 58.—To demonstrate the heat produced by respiration take three tumblers or jars each having a cork with a hole in the centre through which a thermometer is passed. First compare the readings of the three thermometers by placing them together in water at different temperatures. Half fill one jar with soaked seeds (peas, beans, wheat, or barley answer well); the second with seeds that have been killed by boiling (add some corrosive sublimate to the water to prevent growth of moulds or bacteria), the third with moist sawdust (as a control). Place the three jars, with thermometers inserted to equal depth in each, in a box, and put dry sawdust between and around them; cover the whole with a bell-jar or a dry cloth, and compare the readings of the thermometers at the start of the experiment and then at intervals of a few hours.

§ 25 **Movement in Plants.**—Movement may be exhibited (*a*) by the protoplasm of single cells, (*b*) by growing members, (*c*) by fully grown members. The movements are either *spontaneous*, i.e. due to internal causes, or *induced* by the action of external stimuli. The movements exhibited by *fully grown* members, spontaneous or induced, are usually brought about by alteration in the turgidity of cells, and are known as **movements of variation**.

Movements induced by external stimuli are considered fully in Chapter VII. The following are a few examples of spontaneous movements —(*a*) The protoplasm of some cells shows an irregular streaming movement along the primordial utricle and protoplasmic strands, this is known as **the circulation of protoplasm**, and can readily be observed in the cells of the staminal hairs of *Tradescantia*. In other cases there is a more regular movement of protoplasm round the inner surface of the cell wall, this the **rotation of protoplasm**, can be seen in the leaves of *Elodea* and *Vallisneria*, and in *Chara* and *Nitella*. (*b*) The best example of a spontaneous growth movement is that known as **nutation** described in § 27. (*c*) The lateral leaflets at the base of the leaf of *Des-*

modium gyrans show a slow swaying or oscillating movement which goes on so long as the temeprature is sufficiently high A similar movement is exhibited by the lateral leaflets of the Wood Sorrel. The significance of the movement is not known.

§ 26. **Growth** takes place as the visible result of all these metabolic processes The conditions necessary for the healthy growth of a green plant are a supply of food-material, moisture, oxygen, light, a suitable temperature, and a condition of turgidity in growing cells We have to take into account not only the formation of new cells, but also the growth of individual cells.

In the anabolic processes there is the building up of the living substance, and this is accompanied by the storing up of energy. In the katabolic processes there is the formation, from the protoplasm, of certain substances necessary for building up the tissues, or for carrying on the various metabolic processes; the digestion of stored food-material; and the liberation of energy which is made use of in metabolism. Under normal conditions the formation of organic substance and the storage of energy are greatly in excess of the loss of substance and the expenditure of energy. This increase in the total amount, however, cannot be regarded as the distinguishing feature in growth, for, as we have seen, in plants which grow in darkness at the expense of stored material there is a decrease in the total amount.

Growth takes place when there is an increase in size accompanied by a *permanent* change of form as a result of various metabolic and developmental changes.

In many cases we can recognise a *temporary* increase in size without growth taking place, as, for example, when cells become turgid And we may even have the formation of new substance, and yet no growth in the strict sense For example, in a living cell new substances may be formed, and new particles of cellulose be laid down in the cell-wall (thickening of cell-wall) without the cell increasing in size or altering its form.

§ 27. **Properties of Growing-Points.**—(1) Generally, when growth begins in any organ or cell, it proceeds slowly at first, but gradually quickens until it reaches a maximum,

after which it slows down until the energy of growth is exhausted, and the organ or cell acquires its permanent form. The time taken to pass through the whole cycle is called the *grand period of growth*.

At the tips of stems and roots, the growth is greatest, not at the point where there is most rapid division of cells, but at some distance behind this point, that is, the formation of new cells is most abundant at the apex, but the growth and increase in size of the cells take place chiefly at some distance behind the apex. The free end of a root shows several distinct regions, easily recognised (*a*) the growing-point, covered by the root-cap, (*b*) elongating or growing region, (*c*) region bearing roots-hairs, (*d*) thickening region, where also rootlets are produced.

The growth of a bud while it is unfolding affords another example. In the bud the internodes are extremely short. Rapid elongation takes place when the bud begins to unfold. In some cases growth may continue for a long time in the internodes, although they are far removed from the apical meristem, *e g* the lower part of the internodes in Grasses. Similarly, the rapid growth of the leaf is effected when unfolding, although all the cells of the leaf are present in the bud-condition.

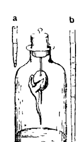


FIG. 111.—GERMINATING PEA, SHOWING GROWTH IN LENGTH OF THE RADICLE.

Exp. 59.—In a jar containing some water fix a soaked bean or pea by means of a long pin passing through the cork and cotyledons (Fig. 111). Observe the escape of the radicle and its downward growth. When the radicle is about an inch long, mark it by Indian ink lines, starting at the tip and making a transverse line every 2 mm. ($\frac{1}{12}$ in.) or 3 mm. ($\frac{1}{8}$ in.). Replace the seedling in the jar, and notice that after a day or two the lines are no longer the same distance apart, but that those near the apex of the root have longer interspaces between them. Further examination will show that growth in length takes place almost entirely in the region just behind the root-cap, and gradually decreases in the regions farther removed from it.

Exp. 60.—Make similar observations with stems, putting the marks ¼ inch apart. Suitable plants are Sunflower and Bindweed (*Polygonum Convolvulus*).

(2) The elongation of the growing point (stem or root) is not in a straight line. As it elongates the growing point may move from side to side in a zig-zag course, or describe a spiral. The reason is that growth is not equal all round the growing point. If the growth is more rapid, first on one side and then on the other, the zig-zag movement is produced. The spiral or revolving movement is due to a wave of more rapid growth passing round the growing apex This movement, of whatever kind, is called **nutation** or **circumnutation.** It is of importance in tendrils, where the revolving movement brings the nutating part in contact with a support round which it coils. The coiling of the tendril round the support is a movement induced by the stimulus of contact (see p 211).

Leaves (and other dorsiventral organs) show a phenomenon somewhat resembling nutation. During the early stages of growth the lower or dorsal surface grows more rapidly than the upper. This phase of growth is known as *hyponasty*, and in consequence the leaves are folded up in the bud condition Later the upper surface grows more rapidly (*epinasty*) and the leaves unfold. We may compare with this the growth of the plumule in many germinating seeds In the Bean, for example, one side of the plumule at first grows faster than the other (*hyponasty*). This causes the arched form in which the plumule reaches the surface of the ground, being thus guarded from injury. The other side then enters on its rapid period of growth (*epinasty*), and the young shoot straightens out.

(3) The cells at growing points are always **turgid.** There is a rapid osmosis of nutritive substances into the cells This is always the case where metabolic processes are actively going on. The metabolic processes disturb the general equilibrium as regards the distribution of nutritive substance, and at the same time lead to the formation of osmotically active substances. **Hence water with nutritive**

substances in solution are drawn into these cells from neighbouring cells. Turgidity is an essential condition of growth; turgidity brings about temporary changes in form which are rendered permanent by the formation of new substance

A condition of turgidity in living cells causes considerable tension (or pressure) in the tissues, not only at growing points, but also in fully grown members The epidermis, being a firm and rather inextensible membrane, will be stretched to some extent by the turgid cells within, and these again will be compressed owing to the inextensible nature of the epidermis The pith, for example, in stems and petioles tends to expand, but is prevented by the outer tissues.

The tensions may be longitudinal or transverse. The longitudinal tension in a stem may be easily demonstrated by splitting longitudinally the growing apical region of a succulent shoot (*e g* Elder). It will be found that the two halves bend away from each other, more especially if the shoot be placed in water This is due to the elongation of the pith, which will be found to present a convex surface If the root of a seedling Bean be similarly treated it will be found that the halves bend slightly inwards, because, in this case, it is the inner tissues that are stretched. The existence of transverse tension can be demonstrated by removing a complete ring of the outer tissue from a succulent stem; on trying to replace it, it will be found that it does not go quite round owing to the expansion of the inner tissue.

Exp. 61.—Split a Caladium stalk longitudinally into four strips, and notice that each strip at once becomes curved, with the epidermis on the concave side Place some strips in water, others in strong (about 10 per cent) salt solution, and observe the differences in the curvature caused by the changes in the turgidity of the inner tissue—*i.e.* that nearest the centre of the stalk.

Exp. 62.—Take a long petiole of Rhubarb. Cut the ends square and carefully measure its length. Then remove the cortical tissue in longitudinal strips It will be found that these strips are shorter, and the remaining cylinder of pith longer, than the original length of the petiole.

§ 28. **Phenomena connected with Pressure.**—The formation of intercellular spaces is evidently due to differences in pressure and tension in the growing cells. This also partially explains the difference between spring and autumn wood, and the formation of annual rings in the wood of trees. During the summer, when the cambium is active, there is a gradual increase in the transverse pressure in the stem, both the wood inside and the bast outside the cambium being compressed (see p. 106). During the winter, when the cambium is inactive, the pressure is relieved.

Occasionally, owing to this pressure in the secondary wood, the walls of some of the parenchymatous cells of the wood are forced through the pits into the cavities of the wood-vessels. The portion of the cell which bulges into the vessel is cut off by a wall; cell-division takes place in it, and a mass of parenchyma is formed *inside the vessel*. These masses are called **thyloses.** They are formed just before the xylem passes over into *heart-wood*, and help to close the cavities of the wood-vessels.

§ 29 **Rate of Growth in Stems.**—A simple method for the measurement of the rate of growth in length and its distribution has been indicated in Experiments 59 and 60, p 192

The rate of growth in length of a stem may be measured by putting a mark on the older part of the stem, and measuring the distance from this to the apex at regular intervals. It may also be measured by means of an apparatus called the **auxanometer.** A fine cord of plaited silk is attached to the apex of the plant (growing in a pot) The cord passes over a pulley fixed above, and to its other end a weight just sufficient to keep the cord tight is attached. The distance through which the weight descends in a given time indicates the rate of growth. A horizontal needle or index may be fixed to the weight, and the distance read off on a vertical scale. This is the simplest form of the auxanometer. Many refinements are introduced into the more elaborate forms.

The results may be plotted on squared paper With a rapidly growing stem a good curve can be obtained by taking readings every three hours. It is found that if minor irregularities be neglected, there is a more or less regular variation of growth corresponding to the alternation of day and night. Growth increases at night and diminishes during the day. The maximum is apparently

attained in the morning just after the plant is again exposed to light, and the minimum in the evening. This variation of growth during every twenty-four hours is called *the daily period of growth in length*. It represents the influence on growth of variations in light, temperature, transpiration, etc., associated with the alternation of day and night.

Special Modes of Nutrition in Flowering Plants

§ 30 **Parasites and Saprophytes** (see p. 16).—Some flowering plants obtain their food by living as *parasites* or as *saprophytes*. Parasites and saprophytes are distinguished as *total* or *partial*, according to whether they get the whole, or part only, of their food in these ways. Plants which have no chlorophyll are necessarily total parasites or saprophytes, since they cannot use free carbon dioxide, and must obtain carbon in the form of organic compounds.

§ 31 **Total Parasites**.—Flowering plants totally devoid of chlorophyll are rare in India, but *Cuscuta*, *Cassytha*, *Christisonia* or *Balanophora* may at times be met with, especially in the hills.

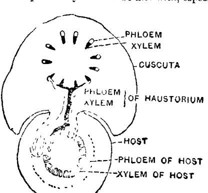


Fig. 111*a*.—Stems of Cuscuta and Host plant in Section, showing a Haustorium.

Cuscuta (Akâshbel) belongs to the Order Convolvulaceæ, and *Cassytha* to the Order Lauraceæ. The flowers in both cases are normal enough, although the vegetative organs are not.

The seedling sends a short root into the ground, while its shoot elongates rapidly and nutates vigorously. Should it meet with a suitable host, it clasps round it, and emits suckers or *haustoria*, which eat their way through to the vascular bundles of the host plant, where the xylem and phloem of the parasite fuse with the corresponding tissues of the plant upon which it is growing (Fig. 111). In this way the parasite obtains its supplies of organic food as well as of water and salts dissolved therein. Meanwhile the *root of*

the parasite dies off, and the plant becomes independent of the soil. Should the seedling not happen to reach a host suitable to its growth, it soon dies. The plant possesses no leaves other than small scales In actual fact it has no use for them.

Christisonia has a short stem which bears reduced colourless scale-like leaves, and is remarkable for the showiness of its flowers, while in *Balanophora* the modification of the plant involved in a parasitic mode of life has gone almost to the furthest degree possible. The plant is parasitic upon the root of its host, and there, except in the flowering season, forms a simple underground tuber, which is not visible from the surface, but in which the material taken from the host is stored up as a reserve, with which at the proper time the plant produces its flowers. These come above the ground in a fairly conspicuous inflorescence, but when the fruit is shed there again remains nothing above the surface, though all the time the tuber is strengthening its hold upon the host by the formation of new or larger suckers Like the other suckers of this class of parasite they are united both to the bast and to the wood.

A yet further stage beyond this leads to the remarkable Order Rafflesiaceæ, found in Java and Sumatra, in which the vegetative body of the plant takes the form of actual hyphæ resembling those of a fungus, and running through the tissues of the host.

§ 32 **Partial Parasites** are plants which contain chlorophyll and have ordinary foliage leaves, so that they can make at least part of their organic food by photosynthesis, while they draw their supply of water and dissolved salts from a host-plant

When the seed of *Loranthus*, or of *Viscum*, the Mistletoe (whose sticky fruits are carried by birds), germinates on the branch of a suitable tree, the radicle penetrates the host, and the woody tissues of the two plants become continuous (Fig 112)

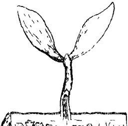


Fig 112. — Young Mistletoe Plant, with Twig of Host-Plant in Section

Several members of the Scrophulariaceæ are partial parasites, e g *Striga* which grows upon the roots of *Sorghum*, and many species of *Pedicularis* which grow upon the roots of meadow grasses They have chlorophyll and ordinary roots, but where their roots come into contact with the roots of grasses, swellings (suckers) are formed, from which parasitic roots grow into the grass-roots The suckers are formed in spring, and through the summer they absorb food from the living grass-roots; during

this time they contain little or no starch. In late summer and autumn organic food is absorbed from the dead grass-roots, and the suckers then store reserve food.

§ 33. **Total Saprophytes.**—Indian examples of totally saprophytic flowering plants are *Monotropa*, *Neottia* and *Epipogum*, all found in the thick leaf-mould (humus) of the forests of Temperate Himalaya. The European species of *Monotropa* is called the Bird's Nest, while *Neottia* is known as the Bird's Nest Orchid.

In all cases the plant is unable to grow in soil which contains no organic matter, and it is enabled to make use of this matter for nutrition by the help of a "fungus-servant" Some of the fungus-threads which permeate the leaf-mould form a dense matting on the surface of the roots of *Monotropa*, and in *Neottia* these threads penetrate the roots and actually grow inside the living cells of the cortex In this way the higher plant is supplied with soluble organic food which it could not absorb in the ordinary way by means of root-hairs

In these two plants it appears that the whole of the food is obtained by the aid of the fungus-threads The fungus by its association with the roots also gains certain advantages—*e g.* shelter from drought—so that the arrangement is an example of **symbiosis**, *i e.* a union or association of two organisms in a common life, both deriving benefit. This particular kind of symbiosis, namely, an association of a fungus with the roots of a higher plant, is called a **mycorhiza.** Symbiosis must be carefully distinguished from parasitism, where one organism lives at the expense of another.

There is no dividing line between total and partial saprophytes, even *Neottia* has some chlorophyll.

§ 34 **Partial Saprophytes** also obtain food by means of a mycorhiza, but since they have green leaves, and therefore carry on photosynthesis, the higher plant is not so completely dependent on its fungus-servant. The roots of most forest trees, and of many other plants which grow in the rich humus of woods and plantations, have an external (*ectophytic*) mycorhiza like that of *Monotropa*, while in Ericaceæ (Rhododendrons, Heaths, etc) the mycorhiza is usually internal (*endophytic*) as in *Neottia*. Most of the plants growing in the peaty soil of heaths and moors have mycorhizas; this is the case, for instance, with moorland grasses, though apparently not with Sedges and Rushes which grow in the wetter boggy parts.

In the case of partial saprophytes, it is probable that the free fungus-threads which project from the surface act as root-hairs, and absorb water and inorganic salts in addition to organic compounds The latter are probably chiefly absorbed for the sake of the nitrogen they contain, since the green plants can absorb carbon dioxide from the air. Plants provided with a mycorhiza produce

few or no root-hairs, since the projecting fungus-threads form a far more effective means of absorbing food-materials.

§ 35. Assimilation of Nitrogen by Leguminous Plants.—The *free* nitrogen of the atmosphere, although abundant, is not made use of by the green plant. There is, however, one important order of flowering plants, the Leguminosæ (the Pea, Bean, Clover order), in which the nitrogen of the atmosphere is *indirectly* used.

It was for a long time recognised that leguminous plants would readily grow in a soil containing little or no *combined* nitrogen, and that as a matter of fact the soil was often richer in nitrogen after a leguminous crop had been grown. These facts, which were at first extremely puzzling, have now been explained. Numerous small nodules or tubercles are found on the roots of these plants. When the tubercles are examined they are seen to be filled with small oval unicellular bodies called **bacterioids** (or bacteroids). These are probably bacteria, although some regard them as the spores of a fungus. They are always present in the soil and infect the roots of leguminous plants through the root-hairs. In the root-hairs they give rise to fine tubes which, making their way into the cortical tissue, stimulate it to active growth and thus lead to the formation of tubercles. The developing tubercles are rich in starch, and later each receives a branch from the vascular bundle of the root.

The bacteroids which are found in the fully grown tubercle are developed inside the invading tubes. Analysis shows that the tubercles are very rich in nitrogenous substances, also in potash and phosphorus, and they seem to develop best in soils which are poor in nitrogen compounds. The tubercles do not develop in plants grown in garden or field soil which has been heated so as to kill any organisms present in it. On the other hand, they grow on roots of plants which have been germinated in garden soil and then placed in culture solution.

There can be no doubt that we have here an example of symbiosis. The bacteroids apparently make use of the free nitrogen of the air, and bring it into combination, just as some bacteria in the soil do (p. 164), and it is probable that, while the leguminous plant gets the benefit of the nitrogen-compounds (nitrates) formed, the bacteria are supplied with carbohydrates (sugar) manufactured by the green plant. The arrangement may be regarded as a special kind of mycorhiza.

§ 36. Carnivorous or Insectivorous Plants obtain part of their nitrogenous food by catching insects in various ways, by means of modified leaves, and afterwards absorbing the soft parts of the insects. Among the Indian insectivorous plants are *Pinguicula*, *Drosera*, *Utricularia*, and *Nepenthes*.

Pinguicula (the Butterwort) is represented in India by *P. alpina*,

occasionally met with in the alpine Himalaya. The plant has a basal rosette of broad leaves, whose upper surfaces are covered with sticky glands, while the margins are rolled inwards slightly. Small insects are caught by the sticky secretion and washed by rain to the edge of the leaf, which curls inwards and encloses them; the glands secrete digestive ferments, absorb the products, and then the leaf becomes unrolled again.

Two species of *Drosera* (Sundew) are fairly common in India, *D. Burmanni* in the plains, and *D. lunata* in the Himalaya and the Nilgiris. Fig. 113 shows the common European species, *D. rotundifolia*. The leaves bear numerous stalked glands or tentacles which secrete a sticky fluid (Fig. 113). If an insect adheres to the tentacles, they bend down upon it and pour out a fluid which has the power of digesting, and rendering soluble, albuminous or proteid substances (white of egg, meat, etc.) in a similar manner to that occurring in the stomach of an animal. The secreted fluid is re-absorbed, together with the soluble nitrogenous products (peptones). When digestion is completed, the tentacles resume their former position, and are then ready to capture another insect. The tentacles may be stimulated to movement by continued contact with any solid substance, but apparently no digestive fluid is secreted unless a suitable organic substance—*e.g.* a piece of raw meat or of boiled egg-albumen—is placed on the leaf.

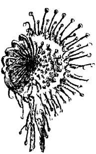


FIG. 113.—LEAF OF DROSERA.
Tentacles expanded on the right, partially inflexed over an insect on the left.

The Bladderwort (*Utricularia*) is a submerged water-plant which has no roots; the submerged parts show no clear division into leaves and branches, but are finely divided, and the flowering shoots project above the water. The submerged parts bear curious bladders, each with a trap-door or valve which is easily opened by a push from the outside, so that small animals (insects, water-mites, water-fleas, etc.) cannot escape once they have entered the bladder. When these animals die, their soft parts decay, and are absorbed by branched hairs which occur on the inner surface of the bladder. Several species of *Utricularia* are found in rice-swamps and tanks all over India, both in the plains and in the hills.

Venus' Fly-trap (Fig. 114) is a native of Carolina, where it grows in peat-bogs; it is often cultivated in hothouses. The leaves are two-lobed, and the midrib acts as a hinge. Each lobe bears on its upper surface three long sensitive hairs. When one of these is touched by an insect, the two lobes of the leaf snap together and capture the insect. Digestion occurs as in Sundew. The leaves of

Venus' Fly-trap are only slightly sensitive to chemical stimuli, but if the closing of the lobes has been caused by an insect they press tightly against each other and hold the insect fast, whereas the

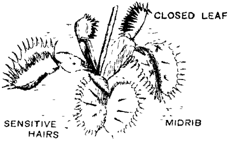


FIG. 114.—VENUS' FLY-TRAP (DIONÆA MUSCIPULA).

closing remains incomplete, leaving a wide space between the lobes, if the hairs have been touched by, say, a pencil. In the latter case the leaf opens again, but if an insect has been caught the leaf remains closed until the digested products have been absorbed.

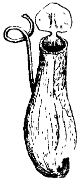


FIG. 115.—PITCHER OF NEPENTHES DISTILLATORIA.

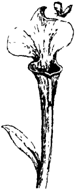


FIG. 116.—PITCHER OF SARRACENIA.

In the Pitcher Plants, of which *Nepenthes* (Fig. 115) is the best known example, the whole or a part of the leaf is developed as a pitcher, with a lid attached to one side of the opening. The pitcher

may be regarded as a long tubular peltate lamina. The bottom of the pitcher contains water, usually swarming with bacteria, and, in *Nepenthes*, a digestive fluid (pepsin) is secreted, so that the insects falling into the liquid are first drowned and then digested. The genus is well represented in the Malay region, but one species also occurs in the Khasia hills, and one in Ceylon.

In *Sarracenia* (Fig. 116) there is no ferment; the bodies of the insects are decomposed by the action of bacteria, and the soluble products absorbed. This genus is exclusively American.

In these and other Pitcher Plants the lids of the pitchers are often brightly coloured and serve to attract insects, but they have no power of movement, and cannot close when once they have opened. The rim of the pitcher also bears honey-glands, which help in attracting insects; below the rim there comes a zone covered with small glands sunk in pits on the inner surface of the pitcher, then comes a smooth slippery region, the lower part of which has hairs pointing downwards, and finally the lowest part containing water. Insects crawling over the gland-bearing upper region soon reach the slippery zone, and are prevented by the hairs below this from crawling up again, so that they eventually fall into the liquid and are drowned.

Most insectivorous plants have enough chlorophyll to enable them to make all the organic food they need, and they can grow quite well when not supplied with insects. When fed with insects, raw meat, or boiled egg, however, the plants become stronger, flower more freely, and produce *stronger and more numerous seeds*. Most insectivorous plants grow in poor swampy soil, which is usually deficient in nitrates and other available nitrogen-compounds. By the capture and digestion of insects they obtain supplies of nitrogenous food independently of the soil, and can in this way grow in localities which would otherwise be unsuitable.

CHAPTER VIII.

THE PLANT AND ITS ENVIRONMENT.

§ 1. **Irritability** is one of the fundamental properties of protoplasm; in other words, it belongs to the nature of living protoplasmic substance that it is capable of receiving impressions from, *i e.* of being stimulated by, various external influences and of making certain responses to these stimuli. The consideration of this fundamental property opens up the whole question of the plant's relation to its environment. It is this property which brings the organism "into touch" with its surroundings. On it ultimately depends the harmony which is everywhere exhibited between a plant and its environment.

The mature organs of plants, in many cases, make responses to the action of external stimuli, but such responses are best exhibited by the *growing* organs. In growth the vital activity of the protoplasm is constantly subjected to, and modified by, the stimulating influence of external agencies.

The response made is commonly of the nature of a movement more or less definite Such movements due to external stimuli are called *induced movements*, and are to be distinguished from the spontaneous movements referred to on p 190.

§ 2. **Stimuli.**—By a stimulus is meant any disturbing external influence which excites a response on the part of the plant. We have seen that a suitable temperature, a supply of oxygen and water, and also frequent exposure to light are essential conditions of healthy development in ordinary green plants. The vital functions cannot be discharged at all when they are wanting. The irritability of the protoplasm also depends on these conditions. This

normal influence of light, etc., on which all vital activity depends, may be spoken of as a *tonic* influence. Apart from this, however, a stimulating influence may be exerted when any one of these factors varies or alters in any way. Other stimuli are gravity, and mechanical contact or pressure; and plants can also respond to various chemical stimuli.

§ 3. **Light.**—The protoplasm of a green plant, as we have indicated above, is in a healthy condition—a condition of *tone*—only if sufficiently exposed to light. The protoplasm loses its irritability, and a pathological condition is established, if the plant is kept for some time in darkness. The healthy condition due to sufficient exposure to light is known as *phototonus*. For each plant there is a certain intensity of light for which this healthy condition is best established. We have more especially, however, to consider the stimulating action of light.

(*a*) *Paratonic Influence of Light.*—Variation in the intensity of light acts as a stimulus on plant members (mature or growing). This is spoken of as the **paratonic** influence of light. It is well shown by the action of light on the chloroplasts in the palisade cells of leaves. In diffuse light the chloroplasts place themselves along the outer and inner walls of the cells and are therefore as freely exposed as possible to the light. This arrangement, or rather this movement by the chloroplasts, is called **epistrophe**. In bright light the chloroplasts place themselves along the lateral walls of the cells and are therefore more or less screened. This is **apostrophe.** The biological import of this will be evident if the student remembers that intense light causes decomposition of chlorophyll.

Again, movement is in many plants induced by the variation in intensity of light associated with the alternation of day and night. Many leaves which are freely expanded during the day droop and turn their edges upwards at night; if the leaves are compound, the leaflets close up. These variation movements (p. 190) are spoken of as **nyctinastic movements** or "*sleep-movements.*"

We have examples in the leaves of the Sensitive Plant, Wood Sorrel, Bean, and Clover. The drooping or closing-up of the leaves is brought about by a change in the turgidity of the parenchymatous cells of the pulvinus (p. 132). The significance of the movements is that at night the leaves lose less water by transpiration, and are protected from cold

The same or similar movements may be induced in these plants during the day by increased illumination. When the light becomes too intense the leaves either assume the drooping night position, or bend upwards and present their edges to the light. In this position (known as "*diurnal sleep*") the leaves are protected from the heating effects of the sun, and the chlorophyll from the decomposing action of light.

In many flowers also movement is induced by variation in the intensity of light. Thus the flower of the Red Campion and the inflorescences of the Daisy and Dandelion close at night. Other flowers like the Evening Campion close during the day when exposed to bright light, and open at dusk The significance of the movements which are brought about by unequal growth of the lower and upper surfaces of the floral leaves (they are not variation movements) is explained, partly by the necessity for the flowers being protected from marauding insects and from various injurious external influences (wet, cold, etc), partly by the conditions of pollination by insects

The general paratonic influence of light is to retard the rate of growth in length of stems, roots, and leaves. Larger leaves and longer stems are found in shaded plants than when exposed to bright light. This has reference, of course, to plants which are in a healthy condition, for which a certain amount of light is necessary. When green plants are grown continuously in darkness, a pathological condition is established (the etiolated condition, p. 177), in which the stems grow enormously in length at the expense of the leaves

(*b*) *Heliotropic Influence of Light*.—Light also exercises a stimulating influence on the *direction of growth*.

This influence depends, not on the varying intensity of light, but on the direction of the incident rays. Speaking generally, radial members tend to place their long axes parallel to the incident rays. This may be effected in two ways. The apex of the growing member may grow either *towards*, or *away from*, the light. Here we are considering the phenomena of *heliotropism*.

Heliotropism may be defined as the response made by a member, as regards the direction of its growth, to the stimulating influence of light. There is **positive heliotropism** if the member turns towards the light, **negative heliotropism**, or *apheliotropism*, if the member turns away from the light. Most radial stems and centric leaves are positively heliotropic, most roots are negatively heliotropic.

A good example of heliotropism is seen when a plant is grown in a window. It will be noticed that, unless the plant be constantly turned round, the stem bends over towards the light. This was formerly ascribed to the retarding action of light on growth. It was thought that the bending was due simply to the shaded side growing faster. No doubt the convex side of the stem does exhibit more rapid growth, but the explanation given is inadequate, seeing that it fails to account for the phenomena of negative heliotropism. All we can say is that these members, under the stimulating action of light, respond by tending to place their long axes parallel to the incident rays. We cannot here enter on the deeper question as to why this should be so.

The behaviour of bifacial leaves and other dorsiventral organs is different. They usually respond by tending to place their surfaces at right angles to the incident rays. This is called **diaheliotropism.**

With regard to the biological significance of the phenomena of heliotropism there is no difficulty. The stem, by bending over towards the light, supports the leaves in the most favourable position for receiving the light. This is seconded by the diaheliotropism of the leaf. The root, by being negatively heliotropic, has the best chance of reaching the soil.

During their growth plant-members take up a definite light-position, which, except in cases where the adult members can exhibit movements, is a fixed one. It has to be noticed that the *fixed light-position* assumed by leaves is such that they turn their ventral (upper) surface in the direction not of the brightest light, but of the brightest *diffused* light to which they are exposed. Most leaves, therefore, if the plants are growing freely exposed to light, are more or less nearly horizontal. But, if plants grow exposed to light of great intensity, this position may be departed from, and the fixed light position may even be a vertical one in which the surfaces are directed east and west as in the "Compass Plants" *Silphium laciniatum* and *Lactuca Scariola*. This vertical position is often found in the leaves of tropical plants, and it is also characteristic of phyllodes (p 147). It has the same significance as the position assumed by mature leaves in "diurnal sleep" (p. 205).

The rays of light which are chiefly concerned in producing these stimulating effects (paratonic and heliotropic) are the blue and violet rays

Exp 63.—Put a Geranium or Sunflower, which has been growing out of doors, in a pot, and set the pot in a window exposed to a good light. Observe in a few days the position assumed by the younger leaves, and the growing region of the stem.

Exp. 64.—Cover a glass jar outside with black paper or cloth, leaving a narrow vertical chink on one side Pour a little water into the jar, and fix a bean seedling to a long pin passing through the cork (see Exp 59, p 192). Place the seedling horizontally and at right angles to the chink. Expose the jar to light, and observe after a day or two that the shoot bends towards the chink, the primary root away from it.

Exp 65.—Pass the roots of germinated Cress, Radish, or Linseed through holes in muslin tied over a tumbler filled with water. Set the tumbler close to a window, or in a box with a vertical slit in the side turned to the light Observe the direction in which root and shoot grow with regard to the light.

Exp. 66.—Show that "sleep-movements" may be induced in the daytime by covering a Clover plant (growing out of doors or in a pot) with an opaque vessel, and heaping soil round the rim to exclude all light

§ 4 **Gravity.**—The force of gravity also has a stimulating influence on the growth of plant members. Under the action of this stimulus primary roots tend to grow down in the direction of the force, primary stems up in the opposite direction.

When a seedling is placed in a horizontal position and protected from the action of light, it is found that curvature takes place in the growing region of stem and root, so that the former turns upwards, the latter downwards. It has been proved that it is the tip of the root that is the irritable region; but the curvature, which takes place with considerable force, occurs in the region behind this, where the cells are rapidly elongating. The same is true of the stem. It must be clearly understood that the curvature is not due in any way to the weight of the part, but that the force of gravity in some way or other stimulates the protoplasm of the growing region and excites a definite response.

The response made by growing members, as regards the direction of their growth, to the stimulating influence of gravity is called **geotropism**. Primary roots are positively geotropic; most radial stems, and vertical leaves are negatively geotropic. It is evident that, when a stem or root shows geotropic curvature, there is increased growth on one side, and retarded growth on the other. Thus, when a seedling is grown in a horizontal position, and curvature of root and stem occurs, it is the upper surface in the root that grows faster, the lower surface in the stem.

Dorsiventral members (*e g* leaves, creeping stems, lateral branches of some trees) make a different response to the stimulus of gravity. They tend to place themselves at right angles to the direction of the force, and are said to be *diageotropic*. Leaves, however, respond more strongly to the directive influence of light than to that of gravity. Lateral roots are also usually regarded as more or less diageotropic, but, as a matter of fact, they are scarcely influenced by gravity; they grow outwards from the parent root, and may be described as *exotropic*. The advantage of this is obvious; it enables the root-system to occupy, as thoroughly as possible, the part of the soil in which the plant is growing.

That the opposite tendencies of primary root and stem referred to are to be ascribed to gravity has been determined by experiment. There is a machine called the **clinostat** consisting essentially of a vertical plate or disc mounted on a horizontal axis. A plant is attached to the disc so that its axis is horizontal, and the disc

rotated *slowly*. A little reflection will show that the normal influence of gravity is eliminated, as each side of the axis is, in turn, directed downwards. It is found that stem and root grow in the directions in which they are placed.

Another experiment is to attach a plant to a wheel which rotates *rapidly* and *horizontally*. Here another force—"centrifugal force"—somewhat similar to gravity, comes into play. If the opposite tendencies of root and stem are to be ascribed to gravity, we should expect similar tendencies to be exhibited under the action of "centrifugal force." This is the case, for under the combined action of gravity and centrifugal force the root bends obliquely outwards, the stem obliquely inwards.

Twining stems show another form of geotropism. When the young slender stem of a twining plant bends over it is not the upper or lower surface which grows faster, but either the right side or the left side. The result is that the stem begins to sweep round in a widening circle. This is known as **lateral geotropism.** The revolving motion gives the stem a chance of reaching a support. The twining of the stem is partly due to the same cause, but that negative geotropism also plays a part is indicated by the upward growth of the stem on the support.

In most cases twining only occurs round supports which are more or less erect, and are not above a certain thickness, for the stems of twining plants have a strong tendency to ascend directly upwards by the shortest possible path. In most twiners, *e.g.* the Convolvulus (*Calystegia sepium*) and Scarlet Runner, the direction of twining, as seen from above, is opposite to the hands of a watch; but in a few, *e.g.* Hop, Black Bryony, and Honeysuckle, it is in the same direction.

Exp. 67.—Fix a seedling Pea inside a glass jar containing a little water so that its axis is horizontal. Cover the jar so as to exclude light. After a day or so observe the curvatures of root and stem. The region of curvature may be determined by marking the root with Indian-ink, as described in Exp. 59, p. 192.

Exp. 68.—Get a test-tube with a cork, and to the cork pin a Pea seedling with a straight radicle 2 inches long; put a strip of blotting-paper in the tube, and run in water to soak it. Fix the seedling in the tube with its radicle pointing to the closed end, and keep the tube inverted so that the radicle points vertically upwards. Observe after a time that the tip of the radicle bends over so as to be directed downwards. Repeat the experiment, but first with a razor cut off the extreme tip of the radicle. Notice if any curvature follows.

Exp. 69.—Grow Bean or Pea seedlings in a box with a glass front sloping downwards and inwards. When the secondary roots have grown out, mark on the glass the positions of a few of these, also of the main root; note especially the position of the *tip* of each root. Then tilt the box up at an angle of about 45°, and notice how main root and side roots change their direction of growth.

Exp. 70.—Fix a seedling Pea or Bean to the side of a small dish containing mercury with a layer of water upon it. Let the primary root lie horizontally in the water. After a time observe that the tip of the root bends over and grows down into the mercury, notwithstanding the resistance offered by the latter owing to its high specific gravity.

Exp. 71.—Grow a Scarlet Runner seedling in a pot, tying the lower part of the stem to a stick, and when about 6 in. of the stem project beyond the stick bend this free part over so that it hangs horizontally. Place a sheet of paper below the pot and draw lines radiating from the centre of the pot; then find the direction in which the free part of the shoot points, and notice the rate at which it swings round. A healthy plant will make a complete circle in about two hours. Provide a similar seedling with a long stick, and notice that the direction of climbing is the same as that of the swinging movement of the free end.

§ 5. **Hydrotropism.**—Roots are sensitive to variations in the amount of water in their neighbourhood. They respond by bending in the direction of the water, and are therefore *positively hydrotropic*. Here also the tip of the root is the sensitive part. The presence of water is a more powerful stimulus than the force of gravity.

Exp. 72.—Grow seeds in wet sawdust in a box with a bottom of wide-meshed wire gauze. Hang up the box obliquely. Under the stimulus of gravity the radicles grow down through the gauze into the dry air, but, owing to hydrotropic influence, they soon curve back and grow along the surface of the gauze.

§ 6. **Contact.**—It can often be observed that mechanical contact acts as a stimulus to many plant-organs. This sensitiveness to contact is well shown by root-tips, tendrils, and one or two twining stems (*e.g.* Dodder).

When a growing root encounters some obstacle, *e.g.* a stone, its growth is so stimulated that it becomes convex at the point of contact and thus is turned away from the obstacle.

When a tendril, in the course of its nutating movement (p. 193), touches some object it becomes concave at the point of contact. This is due to the stimulus being transmitted to the opposite side of the tendril, there producing increased turgidity and growth of cells. More of the tendril is thus brought into contact with the object, and, if the latter forms a suitable support, the process is continued and the tendril twines round it. At the same time the part of the tendril below the point of attachment becomes spirally coiled, and strengthened by the lignification of the tissues. Since the tendril is fixed at both ends during coiling, it follows, from purely physical reasons, that, if a right-handed spiral is formed in the upper part, there will be a reversed or left-handed spiral in the lower part. This coiling of the tendril below the point of attachment not only serves to raise the plant, but also acts like a spring in diminishing the effects of strain or shock.

Some tendrils are sensitive at all points. Others show a curved hook-like extremity, sensitive only on the concave side. Tendrils, unlike most twining stems, may attach themselves to supports inclined at a considerable angle to the vertical.

The leaves of Drosera and Venus' Fly-trap are sensitive to contact. In the Barberry the stamens are sensitive at the base and spring up when touched by an insect. When the leaf of the Sensitive Plant is touched the leaflets close up and the whole leaf hangs down (the normal night position—see p. 205).

Exp. 73.—Notice that young tendrils of Vetches, Sweet Pea, White Bryony, etc., which have not yet become attached, show a slight hook at the free end. Rub the concave side of the hook with a pencil, and notice that this part soon begins to curve (White Bryony and Passion-flower show this very quickly), and in a few minutes form a complete coil. Rub the outer (convex) side of the hooked end of another young tendril, and notice that no bending occurs; the convex side is not sensitive to contact.

Exp. 74.—Fill a glass funnel with moist soil or sawdust. Plant some seeds close to the glass near the top of the funnel, and fix various obstacles an inch or so below them. Notice that the roots diverge from their course only so much as is absolutely necessary to avoid the obstacles, and resume their original course as soon as they have passed one.

Exp. 75.—With the point of a knife remove a small portion of the yolk of a hard-boiled egg, and apply it to one side of the tip of the radicle of a Bean-seedling; fix the seedling vertically in a jar containing some water at the bottom, and keep in darkness. After a few hours, see whether any curvature has taken place, and, if so, in what direction. The one-sided irritation, due to the presence of the foreign substance, exerts a stronger influence than that of gravity, and causes the bending of the root.

§ 7. **Heat,** like light, exerts a tonic influence on plants If a plant is exposed to an unsuitable temperature the protoplasm loses its irritability and all vital processes cease.

There is for each vital process in the plant (respiration, photosynthesis, etc) a *minimum* temperature at which it begins, and a *maximum* temperature at which it ceases, provided the other conditions necessary for the process are fulfilled The range of temperature for each process differs in different plants Speaking generally, for plants in temperate climates, the range of temperature within which vital activity can manifest itself, is from about 0° C to about 50° C Any marked fall or rise of temperature beyond this range inhibits the action of the protoplasm, either by freezing it or by coagulating it

The belief is current that there is also a certain *optimum* temperature, between the upper and lower limits, at which each process goes on most actively. In the light of recent research, however, this view can no longer be maintained Each vital function of the plant is a complex process governed by the presence of a plurality of factors, the action of each factor depending upon the presence of *all* the others Thus light, CO_2, and heat are essential for photosynthesis, and just as the strength of a chain is limited by its weakest link, the amount of photosynthesis will be limited by the factor which is present in the least efficient quantity An increase of the temperature alone, or even of both temperature and light, may not lead to any appreciable increase in the amount of photosynthesis. But as soon as we increase the CO_2 supply also, there is a sudden increase of photosynthesis the CO_2 supply was acting as **a limiting factor.** A little careful thought will show that we cannot speak of the independent efficiency of a solitary factor in a function which is governed by a number of factors.

The death of the protoplasm by cold or heat depends largely on the amount of water present. As a general rule, the greater the quantity of water present the more easily is the protoplasm injuriously affected by extremes of temperature.

Sudden variation of temperature may act as a stimulus. The flowers of Tulip or Crocus, for example, open when there is a rise of temperature. When the temperature falls the perianth leaves fold together again. The movement is due to the fact that above a certain temperature the inner surfaces of the perianth leaves grow more rapidly than the outer, so that the leaves spread apart. At a lower temperature the reverse effect is produced; the leaves slowly fold together, causing the flower to close, and thus to a large extent protecting the essential organs from the effects of frost. The opening movement is usually more rapid than the closing one, owing to the more rapid growth at the higher temperature.

Exp. 76.—Place some dry beans in a dry test-tube, and others which have been soaked in water for two days in a test-tube half filled with water; cork both tubes, and immerse them in a beaker placed on a sand-bath and kept at 60° C for two hours. Try several different temperatures and times. Then soak the dry seeds in water for a day or two and sow both lots Carry out the experiment again, using a mixture of ice and salt instead of hot water. The results of these experiments will show that dry seeds can withstand high or low temperatures that are fatal to soaked seeds.

§ 8 **Chemotaxis**, or sensitiveness to chemical stimuli, is shown by the leaves of Sundew and Venus' Fly-trap (see p. 200). Other examples are found on pp 267, 404.

§ 9 **Mechanism of Movement.**—It is probable that in all cases of movement or curvature stimuli produce their effects by inducing a molecular change in protoplasmic substance, and thus bringing about an altered condition of turgidity This is certainly true so far as the movements of mature organs are concerned (movements of variation), but it probably also holds good for growing organs where the curvatures are due to inequality of growth on the two sides of the growing organ, for, as we have seen, turgidity is an essential condition of growth.

Sometimes the effects produced are clearly out of all proportion to the stimuli This can be explained only by concluding that the effects of a stimulus may be transmitted to a considerable distance from the point of origin There is difference of opinion as to how this is effected In the case of variation movements it can be explained as due to hydrostatic pressure brought about by water being forced from the cells into the intercellular spaces. According

to some, however, in these and other cases the stimulus is transmitted by means of the living protoplasm of the cells, which thus discharges a rudimentary nervous function.

§ 10 **Germination of a Seed.**—We give here a summary of the phenomena presented in the germination of a seed, as they illustrate some of the more important processes with which we have been dealing in this and the preceding chapters The conditions necessary for germination are:—moisture, access of air, a suitable temperature (p. 64)

The seed absorbs a large amount of water and begins to swell Given a suitable temperature, chemical changes are initiated inside the seed Ferments are produced and the digestion of storage food-material begins Oxygen is absorbed and katabolic processes are active. The living protoplasm builds up its substance at the expense of the soluble products of digestion, and rapid growth takes place. The seed-coat is ruptured The primary root grows out; being negatively heliotropic and positively geotropic it grows down into the soil, and produces branches and root-hairs. The plumule escapes from the seed, owing to the elongation of either the hypocotyl or the stalks of the cotyledons, and, being positively heliotropic and negatively geotropic, grows upwards, and comes above ground. In the presence of light, chlorophyll is developed and carbon-assimilation begins

§ 11. **Adaptation to Environment.**—We have now seen that plants can respond to external influences. The responses so far considered have taken the form of movement or curvature of various kinds, and sufficient has been said to show that they are not erratic and meaningless, but have a profound biological significance. But plants respond in many other ways to their environment, all more or less significant, and apparently purposive Indeed, the whole structure and organisation of plants may be regarded as giving evidence of such response, for it is believed that the wonderful adaptation, which is everywhere exhibited by plants as a whole, as well as by individual plant members, has arisen during the course of ages through the

constant interaction between plants and their environment.

We cannot at present enter into this wider question of the adaptation of plants to their environment (see Chaps. XVIII and XIX.). It will be convenient, however, to give here a few general examples, more especially as, by so doing, we can bring together various points that have been incidentally touched on in previous chapters

Adaptation of Leaves.—Consider the adaptation of an ordinary bifacial foliage-leaf Its flattened form gives it a large surface and enables it to absorb the necessary supply of carbon dioxide. It is held in the position which is most favourable for catching the rays of sunlight The epidermis, which has a more or less well-developed cuticle, often also a layer of wax (bloom), prevents excessive evaporation. Both palisade and spongy mesophyll cells, containing numerous chloroplasts, are adapted for assimilation The palisade tissue towards the upper surface is adapted to protect the plastids from the effects of too bright light. The spongy tissue, with numerous spaces communicating with stomata on the under surface, is specially fitted for carrying on the processes of respiration and transpiration The spreading veins convey watery solutions to all parts of the mesophyll, collect the elaborated products, and at the same time serve in the best way to support the leaf-tissue. This supporting and strengthening function is also discharged by ribs or masses of sclerenchyma developed in the mesophyll

Leaf-mosaics.—The examination of the forms of leaves and of their arrangement affords an interesting study in adaptation. In trying to find reasons why leaves have such varied forms and arrangements the main fact to remember is that leaves require to catch as much sunlight as possible, especially in countries where the number of hours of sunlight is limited

In many British plants the leaves tend to fit together like the bits of glass in a mosaic, so as to avoid shading each other and to lose as little sunlight as possible. This tendency is easily seen in plants whose leaves are crowded together and form a rosette close to the ground—*e g* Daisy, Hawkweed, Plantain, London Pride, in many plants with whorled leaves—*e g* Woodruff, in twigs of many trees —*e g* Horse Chestnut, Beech, Elm, Lime, in twigs of plants which creep along a wall or bank—*e g* Ivy. This may perhaps be correlated with the fact that the growth of a leaf largely depends on the amount of light it receives

At the same time it is necessary to bear in mind that other factors influence the shape and arrangement of leaves, *e g*, the necessity of being able to withstand high winds, to carry away rain which falls on the blade, etc. We frequently find, for example, that the leaves are adapted by the possession of grooved petioles,

auricled base, etc., to conduct rain-water inwards to the stem down which it trickles to the ground; while in other plants the lower leaves have longer petioles and all the leaves have acuminate apices, so that the rain-water drips from leaf to leaf and is conducted outwards.

Spines, Prickles, and Hairs.—Prickles serve to protect the plant; but they often do more, especially when they curve downwards as they do in the Rose and the Bramble, for in this case they are so many hooks that help to support the stem, and therefore assist the plant in climbing among the surrounding bushes and herbage

Glandular hairs are frequently sticky; in this case they are of use as a protection against obnoxious creeping insects, which are frequently caught and retained by the secretion The hairs present on the stem are always cuticularised, and when the cuticularisation is very pronounced they become almost impermeable to water. In such cases they may serve to protect the plant, and especially the young growing organs, from an excessive loss of water.

Hairs, when thickly set, help to cut off sensitive growing organs from excessive illumination, which retards their growth and may injuriously affect them Similarly, a close covering of hairs is of some importance in retaining heat during the night and thus keeping the plant warm, while hairs are also of great value in preventing the surface of the plant from being wetted by rain The Chickweed (*Stellaria media*) has a line of hairs running from node to node down the stem, forming a kind of staircase down which drops of rain roll, so that they are rapidly led away from the upper portions of the stem.

The formation and development of hairs and spines depends to a great extent on external conditions Thus, the same plant that produces these parts when growing in a poor, dry soil fully exposed to the rays of the sun, becomes of a much softer and less aggressive character when grown in a rich, moist soil. Under the former circumstances the plant, by converting some of its buds and leaves into spines, reduces the amount of its foliage, and thus economises its scanty supply of water At the same time the spines serve to protect the plant from herbivorous animals. Many succulent plants, however, which grow in dry situations, such as the Stone-crop (*Sedum*) or the House-leek (*Sempervivum*), show but little tendency to form hairs or spines, since they have other means of checking transpiration (thick cuticle, etc.) The Rest-harrow (*Ononis arvensis*) has no spines when grown in rich, moist soil, but in dry, exposed situations the great majority of the branches end in hard, sharp points.

Water-plants.—In water-plants, since absorption goes on over the whole submerged surface, the epidermis is not cuticularised. Further, as there is no transpiration, no stomata are developed (except on floating leaves, p 59) Correlated with these features

root-hairs and frequently even roots are absent, and the tracheal tissue is poorly developed. The xylem in aquatic stems (e.g. in *Myriophyllum*) is usually central, where it best meets the slight pulling strain due to the water. Support being given by the water there is little or no sclerenchyma. The leaves may be ribbon-like or much divided according as the plants grow in moving or in still water, and, as the chloroplasts need no protection, they are present in the epidermal cells and palisade tissue is absent. Finally the presence of large air-spaces facilitates the passage of air necessary for respiration, and gives buoyancy to the plant.

Xerophytes are plants which show special adaptations for economising their water supply. They are typically met with in dry, hot, sandy regions where the supply of water is uncertain and the conditions favour excessive transpiration; but low barometric pressure at high altitudes and exposure to high winds tend to increase transpiration, while low temperature, excess of salt or humus in the soil, etc, reduce root-absorption, and thus there may be necessity for economy even in cases where water is abundant. Hence xerophytic adaptation is exhibited in varying degrees by plants in very different habitats, e g rock-plants (*lithophytes*), shore-plants (*halophytes*), plants growing on mountains at high altitudes (*alpine plants*), etc

Provision may be made for storage of water by the development of succulent stems or leaves, and for reduction of transpiration by such devices as the crowding of leaves, reduction of leaf surface, the inward rolling of leaf-margins, the formation of a thick cuticle, coverings of hair, the protection of stomata in cavities, etc.

Epiphytes —Plants which are adapted to live on other plants, but are not parasitic, are called Epiphytes. They usually develop clinging roots, which are organs of adhesion, and other roots for obtaining food-material. As their water supply is precarious they often show xerophytic characters. A ready method of seed-dispersal is an evident necessity, frequently the seeds are carried by the wind or by birds. Epiphytes abound in tropical woods and include many orchids.

CHAPTER IX.

STRUCTURE OF THE FLOWER*

§ 1 **General.**—The flower may be regarded as a leafy shoot highly specialised in adaptation to the performance of reproductive functions The function of a flower is essentially to produce seed and fruit, and the various parts (stem and leaf organs) have been specially adapted to the performance of that function It is necessary at the outset to impress this fact on the student Stem and leaf organs in both vegetative shoot and flower have the same *morphological* value, their *physiological* value only is different It must not be inferred however, that the floral leaves have been derived from, or are modifications of foliage leaves

The only essentially new structures in the flower, from the morphological point of view, are the organs—pollen sacs and ovules—which are more immediately concerned in the production of seed These organs may be developed on the floral leaves, or on the axis of the flower They correspond to the spore cases or spore sacs of lower plants, and it is only by careful study of these lower plants that we can arrive at a clear conception of their significance and origin

The axis (stem portion) of the flower usually shows two regions—the **pedicel** and the **thalamus** (also called the torus or receptacle) The pedicel is, popularly, the stalk of the flower It may be present or absent If present the flower is *pedicellate*, if absent, *sessile* The thalamus

* Much of this chapter is intended for reference only The numerous technical terms descriptive of calyx, corolla, etc, can only be mastered when the student has begun the systematic practical study of the Natural Orders

or torus, is the portion of the axis to which the floral leaves are attached. In *typical* flowers there are four sets or series of floral leaves. To the outside are the **sepals**, collectively, they constitute the **calyx**. Internal to these are the **petals**, constituting the **corolla**. Then the **stamens** forming the **andrœcium**; and finally, in the centre of the flower, are the **carpels**, forming the **gynæceum*** or **pistil**.

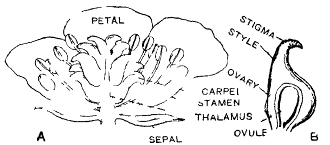


Fig 117 —FLOWER OF BUTTERCUP
A Longitudinal vertical section of whole flower B Longitudinal section of a single carpel

The common Buttercup is a very convenient type for making a first acquaintance with these structures (Fig 117) In the Buttercup the carpels are separate from each other, and *each* shows a hollow basal portion called the **ovary,** above which are the parts known as **style** and **stigma** (Fig 117 B) In the majority of flowers the carpels are united and form a single compound ovary (see Fig 125)

The following facts support the above view of the morphological character of the flower (*a*) The flower like an ordinary foliage shoot arises as a bud very often in the axil of a leaf (bract) (*b*) The thalamus has the general structure of a stem and the sepals and petals in their structure and development resemble leaves (*c*) While in most cases the stamens and carpels having been highly specialised are quite unlike leaves there are certain conditions in

* *Gynœcium* and *gynecium* are varieties of spelling in common use

which they become distinctly leaf-like. Thus, in many cultivated flowers, *e.g.* the Rose, the stamens are transformed into petals; in the Double Cherry the gynæceum is represented by a tuft of small green leaves; in the Water Lily there is a gradual transition between petals and stamens.

§ 2. **The Inflorescence.**—The floral, or reproductive region of the plant is usually distinctly marked off from the foliage, or vegetative region, and is known as the **inflorescence.** Sometimes the main vegetative-axis of the plant passes gradually into a single terminal flower, *e.g.* Tulip and Wood Anemone. Here the flower is said to be **solitary** and **terminal.** In other cases, the flowers are developed singly in the axils of ordinary foliage leaves, and are called **solitary and axillary**. These are very simple types of inflorescence. Usually the flowers are aggregated on a more or less complex branch-system. According to the nature of the branching, and other points, many different kinds of such inflorescence are recognised (*e.g.* Fig 118) These will be specially considered later (Chap. X).

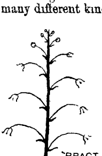


Fig 118.—A Simple Inflorescence (Raceme) The main axis (peduncle) is here the mother-axis. The stalk of the flower is the pedicel.

The main or primary axis of the inflorescence, together with any secondary axes which may be developed (apart from the pedicels of the flowers), is called the **peduncle.** This term is applied instead of pedicel to the stalks of solitary terminal, and solitary axillary flowers If the peduncle is an unbranched leafless axis which arises from the midst of radical leaves and bears flowers at its apex, it is called a **scape,** *e.g* the Onion.

§ 3 **Bracts, etc.** (Fig 118).—When the flower arises as a lateral bud, the axis on which it is borne is called the **mother-axis.** This may or may not be the primary axis of the inflorescence. The side of the flower which is towards the mother-axis (or towards the growing point of the mother-axis) is said to be **posterior;** the side away from

the mother-axis is **anterior.** In a solitary terminal flower it is evident that these terms are not applicable

If the flower arises in the axil of a leaf-structure, this leaf-structure is called a **bract.** Though this may be given as the strict meaning of bract, it is found convenient, in practice, to apply the term to any more or less specialised leaf-structures in the region of the inflorescence, other than the floral leaves themselves.

Bracts or *hypsophylls* present great variety of form and colour. When present, the flower is *bracteate*; when absent, *ebracteate*. The bracts may be ordinary foliage leaves, as in solitary axillary flowers, or more or less resemble them, though differing from the ordinary foliage leaves of the plant Frequently they are small, green, and scale-like In many plants they are reduced to small, tooth-like structures. When they are not green, but coloured like the petals of a flower, they are said to be *petaloid* In many flowers the flower-stalk bears small outgrowths of the nature of reduced leaves These are called **bracteoles.** When present, there are *usually* two in Dicotyledons, placed laterally, and one in Monocotyledons, situated on the posterior side.

§ 4. **Perianth, or Floral Envelopes.**—The outer series of floral leaves, distinct from stamens and carpels, constitute the perianth of the flower. In the great majority of flowers the perianth consists of two series, clearly distinguished as calyx and corolla.

Sometimes calyx and corolla more or less resemble each other, the sepals and petals having much the same form and colour When the two series or whorls are so closely inserted on the thalamus, or so fused together that they look like a single series, the terms calyx and corolla, sepals and petals, are not used, and the whole structure is described simply as a perianth (*e g* Narcissus, Lily of the Valley, and many other Monocotyledons). On the other hand, the perianth may be absent, or represented by a single series or whorl

As the perianth leaves are not essential, but only accessory to the production of seed, they are frequently referred to as the *non-essential organs* of the flower. If one or both series be absent the flower is said to be *incomplete*.

If both series of the perianth are wanting, the flower is **achlamydeous**; if one only is present, **monochlamydeous**; if both are present, **dichlamydeous**. In some flowers (e.g. Daisy, and many other Compositæ) it is recognised, by comparison with allied types, that the calyx has been lost; in such flowers the remaining series must be described as the corolla, not as the perianth. So also, in cases where the corolla has disappeared (e.g. Clematis, Anemone, and many other Ranunculaceæ), the remaining series, although petaloid, must be described as the calyx. The term perianth, however, should be used if the monochlamydeous condition is primitive, i.e. if it is an original or ancestral character and not due to the disappearance or suppression of a second series (e.g. Castor-oil or other Euphorbiaceæ).

§ 5. **The Essential Organs.**—The andrœcium and the gynæceum or pistil, because they bear the reproductive bodies, pollen-grains and ovules, necessary for the production of seed, are called the essential organs.

If both are present *in the same flower* (the rule in Angiosperms) the flower is **hermaphrodite**, *bisexual* or *monoclinous* (symbol ☿). When they are borne on different flowers, as is sometimes found, the flowers are *imperfect*, **unisexual** or *diclinous*. The unisexual flowers bearing the stamens are male (♂) or *staminate*; those bearing carpels, female (♀) or *pistillate*. If staminate and pistillate flowers are borne on the same plant (e.g. Jack), the plant is **monœcious**; if on different plants (e.g. Date and some other kinds of Palm), **diœcious**. A plant is *polygamous* if it bears staminate, pistillate, and hermaphrodite flowers (e.g. Ash). Flowers in which both stamens and pistil have been lost are *neuter* (e.g. ray florets of Cornflower and Sunflower).

§ 6. **Floral Phyllotaxis.**—In most flowers the series of floral leaves are arranged in whorls, and the phyllotaxis is *cyclic*. Sometimes, however, all the floral leaves are in a spiral (e.g. Cactus) and the flower is said to be *acyclic*. If some of the series are cyclically arranged, others spirally, the flowers are *hemicyclic*. In the Buttercup, for example, the calyx and corolla are whorled, while the stamens and carpels are spiral.

§ 7. **Number of Parts.**—We may regard typical flowers as having four definite series or whorls of floral leaves—calyx, corolla, andrœcium, and gynæceum—with the same number in each series. But additional whorls may be developed in any one of these series, so that the number of floral leaves in that particular series is a

multiple of the original number. This is most frequently seen in the andrœcium. On the other hand, the number in any one series may be reduced by suppression or disappearance of one or more of the parts in that series. This is very commonly seen in the gynæceum, which is the most variable part of the flower.

The following examples will illustrate these points.—The Violet has five sepals, five petals, five stamens, three carpels, the Pea has five sepals, five petals, ten stamens, one carpel, the Wall-flower has four sepals in two whorls, four petals in one whorl, six stamens in an outer whorl of two and an inner whorl of four, two carpels; many flowers have a large number of stamens in several whorls (*e g* the Cherry) It should be noticed that owing to the abbreviation of the thalamus and other causes, it is often difficult to distinguish the separate whorls, *e g.* the two whorls of sepals in the Wall-flower, the two whorls of stamens in the Pea.

Neglecting the reduction of parts met with in particular series, and more especially in the gynæceum, we find that in Dicotyledons the series of floral leaves are, *as a rule*, arranged in twos, fours, or fives, or multiples of these numbers In other words, the arrangement is *dimerous*, *tetramerous*, or *pentamerous*, rarely trimerous The *trimerous* arrangement, *i e* in threes or multiples of three, is characteristic of Monocotyledons

§ 8 **Alternation of Parts.**—The general rule is that the leaves of the different series alternate in position with each other—the petals alternate with the sepals, the stamens with the petals, etc If there are several whorls of stamens, these whorls alternate with each other.

But there are exceptions. In spiral flowers, the parts are sometimes superposed. In cyclic flowers the departure from regular alternation arises from various causes In the Primrose Order, for example, there are five sepals, five petals, five stamens, and the stamens are opposite to the petals (*antipetalous*), this is due to the suppression of an outer whorl of five stamens. Sometimes, where there are two alternating whorls of stamens

the outer whorl is opposite the petals. This (the *obdiplostemonous condition*) is due to displacement of the two whorls, which we can easily understand, remembering the abbreviation of the thalmus and the close proximity of the whorls. The carpels, owing to reduction of parts in the gynæceum, frequently have no definite position in relation to the parts of the other series.

§ 9. **Regular and Irregular Flowers.**—In regular flowers the parts in each series have the same size and form, *i.e* the sepals resemble each other, so also the petals, etc. Irregular flowers are those in which some of the floral leaves in any one series have a different shape or size from the others—for example, the petals of Pea or Violet.

§ 10 **Floral Symmetry** (see p 10) —Flowers may be radially symmetrical or *actinomorphic*, *isobilateral*, *zygomorphic*, or *asymmetrical*. The important planes of symmetry are the median or antero-posterior, the diagonal, and lateral planes (see Figs 140, 141) Zygomorphy is very frequently due to irregularity, and this is the sense in which the term is used as a rule in descriptive botany. In zygomorphic flowers the plane of symmetry is, in most cases, antero-posterior or median, *i e* it is the plane passing through the anterior and posterior sides of the flower, *e.g.* Pea, Violet (Figs 143, 144), etc. Asymmetrical flowers are usually spiral, *e g.* Cactus.

§ 11. **The Thalamus—Insertion of Floral Leaves.**—The thalamus is nearly always short or abbreviated Only occasionally is it elongated between the whorls of floral leaves, as in some species of the Capparidaceæ. The form of the thalamus varies considerably It may be convex and more or less dilated, or flattened, or hollow and cup-shaped. The insertion of floral leaves varies according to the form of the thalamus.

In many flowers (*e g.* Buttercup, Campion, Poppy) the thalamus is more or less convex, like the head of a nail. The gynæceum is developed at the apex of the thalamus;

the stamens, petals, and sepals, are inserted, *in order*, on the side of the thalamus below the gynæceum. This is the **hypogynous** arrangement (Fig. 119, A).

Suppose now that the thalamus is not convex, but forms a flattened circular disc. The apex of the thalamus is, of

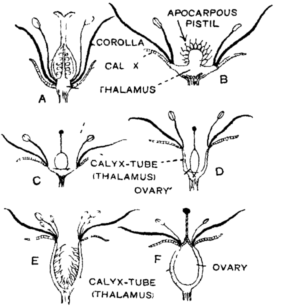


Fig 119 —THALAMUS AND INSERTION OF FLORAL LEAVES.
A, Hypogynous, B—E Perigynous F, Epigynous.
(Diagrammatic vertical sections)

course, in the middle of the disc, and the flattened form is due to the sides of the thalamus having grown up to the same level. The gynæceum is developed in the middle of the disc, and the sepals, petals, and stamens round the rim or margin. They are not *underneath* the gynæceum, but *round about* it. Hence this is called a **perigynous** arrangement (Fig. 119, C). Sometimes the carpels are

borne on a conical protuberance in the middle of the disc; this would represent a continued growth of the apex (*e.g.* Strawberry or Raspberry, Fig. 119, B).

It is with the perigynous condition that the student will experience most difficulty; there are so many degrees of it. The thalamus may not be flat, but hollowed out, and more or less cup-like. This is due to the sides of the thalamus continuing to grow above the apex, which lies at the bottom of the cup (× Fig 119, D). The carpels (gynæceum) are developed in the cup; the sepals, petals, and stamens from the rim of the cup. This also is a perigynous condition. It should be particularly noticed that the cup was formerly regarded as part of the calyx and called the **calyx-tube.** This term is still retained, but the student must be careful to observe that it is the thalamus or receptacle. A still more extreme form of perigyny is found in the Wild Rose (Fig 119, E). Here there is a very deep cup.

Finally, in the **epigynous** condition (Fig. 119, F) the thalamus forms a deep cup as in the extreme forms of perigyny; but the carpels, developed as in the extreme forms of perigyny, are from the first adherent to the calyx-tube, which is for this reason considered as part of the ovary. Thus in epigynous flowers the sepals, petals, and stamens are inserted *on* the gynæceum.* In the perigynous condition the calyx-tube remains distinct from the ovary.

§ 12 **Nectaries.**—The thalamus or receptacle frequently bears a fleshy or glandular outgrowth, such as is found on the top of the inferior ovary in Umbelliferæ and in the common Ivy. This is termed the disc. In the Blackberry the disc lines the outer concave part of the receptacle. Very commonly the disc is lobed (Vine, Wallflower), and frequently it secretes nectar. Nectaries may, however, develop from, or upon, any part of the flower. Thus in the Violet the outgrowths borne by two of the stamens

* The student should notice that, strictly speaking, in epigyny the gynæceum is not formed simply from carpels.

secrete nectar into a hollow spur borne by the anterior petal. In the Buttercup a small projection at the base of each of the petals performs the same function, while the whole of the petals of the Christmas Rose are modified into hollow tubular nectaries. Honey glands occur upon the gynæceum of Gentians, and each sepal of the Hollyhock flower bears a nectary on its inner surface.

§ 13. **The Calyx** may consist of numerous sepals showing a primitive spiral arrangement, as in Cactus and Water Lily, but usually it consists of from two to five sepals.

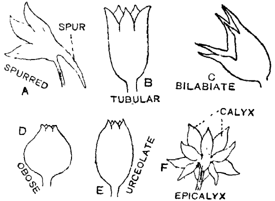


Fig 120 —Forms of Calyx.

If the sepals are free, the calyx is **polysepalous.** When they are united laterally, to however slight an extent, the calyx is **gamosepalous.** The gamosepalous condition is due, not to the actual fusion of originally separate sepals, but to common basal growth during development. In all hypogynous and perigynous arrangements the calyx is described as *inferior*; in the epigynous flower the calyx is described as *superior*.

In some flowers, *e.g.* the Strawberry, the sepals are stipulate. The stipules fuse in pairs between the sepals

and produce an outer series of small sepal-like structures, forming what seems to be an outer calyx. This is known as the **epicalyx** (Fig. 120, F). An epicalyx may also be produced by the aggregation of bracts or bracteoles beneath the calyx, *e g.* the Mallow and Sweet William.

The calyx usually has a protective function. It commonly serves to protect the parts of the young flower in the bud. When the flower opens the calyx may fall off, *e.g.* in the Poppy, in which case it is said to be *caducous*, or the sepals simply fold back as in the Wild Rose. The calyx is *deciduous* if it falls off when the flower withers. But frequently it *persists* till fruiting takes place in order to protect the young fruit, which is developed from the ovary of the flower (*e g* Bean, Strawberry, and Dead Nettle). A gamosepalous calyx not only affords a more efficient protection to the flower-bud than a polysepalous one, but also gives support and protection to the base of the adult flower and to the developing fruit. Hence a gamosepalous calyx is never caducous.

In the Umbelliferæ, where the flowers are closely aggregated, and in many Compositæ, where in addition they are surrounded by a ring of bracts, a protective calyx is not required Hence the calyx is either very small or has disappeared altogether.

The calyx, however, may take on other functions. Thus, in many Compositæ (*e g* Dandelion, Thistle, and Cornflower) there is a rudimentary calyx represented by hairs, forming a silky **pappus** (Fig 124, A), which undergoes further development after flowering, and serves to disperse the fruit. In some flowers also the sepals instead of being green, as is usually the case, are brightly coloured, and usurp the attractive functions of the corolla. In this case the calyx is said to be petaloid.

In a polysepalous calyx the outline of the individual sepals is described in the same terms as are used for ordinary foliage leaves. The number of sepals in a gamosepalous calyx is usually indicated by divisions or teeth (*e g.* Fig 120, B) If the divisions pass almost to the base of the calyx, it may be described according to their number as 3-, 4-, 5-*partite*; if about half way down, 3-, 4-, 5-*fid*; if the divisions are small, 3-, 4-, 5-*toothed*.

But there are special descriptive terms with which the student should be familiar :—

The sepals are *spurred* if they are prolonged downwards into a tubular process, *e.g.* Garden Nasturtium (Fig. 120, A); *saccate*, if pouched or dilated at the base, *e g.* many Cruciferæ. The calyx is *galeate* or *hooded*, if one or more of the sepals form a helmet-shaped structure, arching over the other parts of the flower, *e.g.* the Monkshood (Fig 121). The **gamosepalous calyx** is *tubular* (Fig. 120, B), if regular and elongated with nearly parallel sides; *campanulate*, if regular and more or less bell-shaped (Fig. 124, E); *infundibuliform* or funnel-shaped, if it widens gradually from a narrow base (Fig. 124, B); *urceolate* (Fig. 120, E), if expanded in the middle and narrowing towards base and apex; *globose*, if shorter and almost globular (Fig. 120, D); *bilabiate* (Fig. 120, C), if irregular and drawn out on each side so as to form two lips.

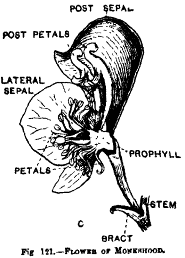


Fig 121.—FLOWER OF MONKSHOOD. Vertical section. Calyx galeate.

§ 14. **The Corolla.**—The primitive corolla consists of a spiral of free non-coherent petals. In most plants this has been changed into a single whorl (Foxglove, Geranium) or, more rarely, a double whorl of petals (Poppy). In Water Lilies and in double flowers the petals are arranged in a close spiral.

The corolla may be *polypetalous* or *gamopetalous* (cf. calyx), *regular* or *irregular*, and as it to a large extent determines the symmetry of the flower, the terms *zygomorphic*, *actinomorphic*, are applied to it. According to the insertion of petals the corolla is described as hypogynous, perigynous, or epigynous.

The corolla is, in most cases, an attractive structure;

its chief function is to attract insects to the flower in connection with the process of pollination It also protects the stamens and carpels at the most critical period of their existence, and this is especially the case when the petals are united together in the form of a tube enclosing the essential organs The tube also serves as a receptacle for honey. After fertilisation the seeds begin to develop, and an attractive corolla being no longer needed, it is usually rapidly shed The withered corolla, however, may persist in a few cases (Currant, Gooseberry).

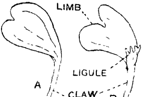


FIG 122—UNGUICULATE PETALS
B also ligulate

The petals are usually brilliantly coloured, sometimes green (sepaloid). They may be absent, e g Lady's Mantle and some Ranunculaceæ (Clematis, Anemone), or reduced to nectar-secreting structures, e g Monkshood (Fig. 121) and Christmas Rose.

In a polypetalous corolla the outlines of the individual petals are described in the same terms as are used for the foliage leaf, and, as in the calyx, the gamopetalous corolla may be described as 3-, 4-, 5-partite, -fid, or -toothed.

The following are some of the more special terms —

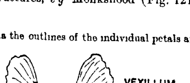


FIG 123 – A, VERTICAL SECTION OF A CARYOPHYLLACEOUS FLOWER; B, PAPILIONACEOUS FLOWER.

The petals are *unguiculate* or clawed (Fig. 122) if they show a distinction into a stalk-like basal portion, the *claw*, and an expanded upper part, the *limb* (e g Wall-flower), *ligulate*, if ligules are developed at the junction of claw and limb (e g. Pink—Fig 122, B); one or more of the petals may be *spurred* (e g Violet); the petals are *fimbriated*, if they bear a fringe of hair-like processes (e g. Mignonette).

The following special terms are applied to polypetalous corollas:— *Cruciform* where the corolla consists of four unguiculate petals arranged crosswise, *i.e.* in the diagonal planes of the flower (*e.g.* Wall-flower and Cruciferæ generally, see Fig. 128, A); *rosaceous* (Fig 119, B, C), if it consists of five spreading petals, not clawed, and attached perigynously (Rosaceæ); *caryophyllaceous* (Fig. 123, A),

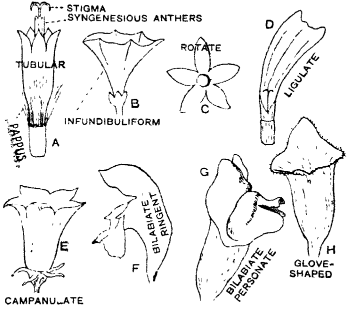


Fig. 124 – FORMS OF GAMOPETALOUS COROLLA.

A, Tubular hermaphrodite; D, Ligulate pistillate, florets of a Composite.

if it consists of five clawed petals, with spreading limbs attached hypogynously to the thalamus inside a slender tubular calyx (Pinks and other Caryophyllaceæ); *papilionaceous* (from the supposed resemblance to a butterfly), if it consists of five petals, one large—the vexillum or standard, two lateral—alæ or wings, and two fused to form a boat-shaped structure—the carina or keel (Pea and other Papilionatæ, Fig 123, B)

Gamopetalous corollas may be *tubular* (Fig. 124, A), *campanulate*, or bell shaped (Harebell, Fig. 124, E), *infundibuliform*, or

funnel-shaped (Fig 124, B); *urceolate*, or urn-shaped (Purple Heath), *globose*, *bilabiate* (for these terms see under calyx, p. 229); *bilabiate and ringent*, if the two lips gape apart (Dead Nettle, Fig. 124, F); *bilabiate and personate*, if the two lips are closed up (Snapdragon, Fig. 124, G); *glove-shaped*, if like the finger of a glove (*e.g.* Foxglove, Fig. 124, H); *hypocrateriform*, or salver-shaped, if it has a *long, slender* tube and a spreading limb (*e.g.* Primrose, Fig 125); *rotate*, or wheel-like, if there is a spreading limb and a very short tube (*e.g.* Forget-me-not, Fig. 124, C); *ligulate*, or strap shaped, if it consists of an elongated membrane which represents the one-sided development of a short basal tubular part (*e.g* Dandelion and other Compositæ, Fig. 124, D).

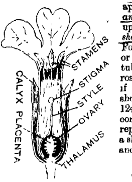


Fig 125.—VERTICAL SECTION OF FLOWER OF PRIMROSE. COROLLA HYPOCRATERIFORM

§ 15 **A perianth**, when not distinguished into calyx and corolla, is described in much the same way; but the terms *polyphyllous* and *gamophyllous* are used to indicate the free and coherent condition, respectively, of the perianth leaves

§ 16. **The Corona.**—This is the term applied to the whole series of ligules developed on the corolla or perianth of certain flowers In Narcissus, where the perianth is gamophyllous, the ligules are coherent, and the corona is cup-shaped.

§ 17. **Prefloration.**—This has already been referred to (see p. 145). The prefloration of the perianth (or calyx and corolla) only can be studied. The ptyxis, or folding of the individual floral leaves, is described in the same terms as are used for foliage leaves (see p. 146) The æstivation of calyx or corolla (Fig. 101) may be *valvate*, *imbricate*, or *contorted* (*twisted*). *Induplicate** æstivation is a form of valvate in which the margins of the floral leaves are folded inwards on themselves. *Quincuncial** æstivation is a form of imbricate where there are five leaves (sepals or petals), two

* Although not mentioned on p 146 valvate *vernation* may be induplicate, and imbricate *vernation* quincuncial.

internal, two external, and one partly internal, partly external. *Vexillary* æstivation, characteristic of the corolla of Leguminosæ, is another form of imbricate æstivation (Fig. 144). The æstivation may be recognised either by taking transverse sections of young flower-buds, or carefully removing the young floral leaves one after the other.

§ 18. **The Andrœcium.**—A typical stamen (Fig. 126) consists of three parts—**filament, anther,** and **connective.** The filament is the stalk of the stamen corresponding to the petiole of a foliage leaf, while the anther may be regarded as representing the lamina of the floral leaf. The latter usually consists of two *anther-lobes*, and

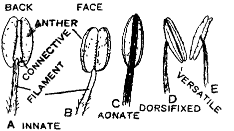


Fig. 126.—Stamens, showing Insertion of Anthers.

forms a case or box in which are contained the **pollen-grains** or essential reproductive bodies. These lie in four cavities, the **pollen-sacs** (Fig. 127), of which there are two in each anther-lobe. When the anther dehisces the partition between the two pollen-sacs in each lobe breaks down, so that there seems to be a single cavity or loculus in each lobe. This fusion often takes place much earlier in the development of the anther.

The anther-lobes are connected towards the back of the anther by a strip of tissue containing a vascular bundle. This is the *connective*. It is usually narrow, so that the anther-lobes lie close together, but may be elongated so that the lobes are widely separated, as in some Labiatæ.

In a few cases (*e.g.* Mallow, Hazel, Hornbeam) the stamens when quite young undergo division or segmentation,

and thus in the fully developed flower the anthers have only one anther-lobe with two pollen-sacs

Sometimes special appendages are developed on stamens. These generally arise as outgrowths of the connective. In the Violet there is a membranous orange-coloured outgrowth on top of each anther, and, in addition to these,

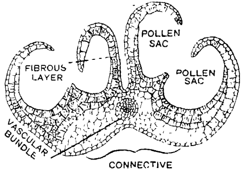


Fig 127 —Transverse Section of Anther of Wall flower, after Dehiscence.

the two antero-lateral stamens have each a green elongated process (functioning as a nectar gland) passing down into the spur of the anterior petal (Fig 143).

Barren or rudimentary stamens are called **staminodes.** They may consist simply of filament or be represented by various peculiarly modified forms.

The stamens may be hypogynous, perigynous, or epigynous; but sometimes, owing to common basal growth, they adhere to the corolla (or perianth). They appear then to be developed on the petals, and are said to be **epipetalous** (*epiphyllous*, if on a perianth) This is found in many gamopetalous, or gamophyllous, orders of Angiosperms, *e g* Compositæ, Labiatæ, Primulaceæ (Fig 125). Sometimes the stamens are adherent to the gynæceum, *e g* in Orchids; this is the *gynandrous* condition.

If the stamens are free from each other, *i.e.* not coherent, the andrœcium is **polyandrous** (diandrous, triandrous, pentandrous, etc., according to the number). If united, the union may be of two kinds. (*a*) The stamens cohere by their filaments: this is the **adelphous** condition—**monadelphous**, if all are united to form a tube round the pistil, **diadelphous** if united in two groups, *polyadelphous* if in several groups. The monadelphous condition is found, for example, in the Mallow and some Leguminosæ (*e.g.* the Broom); the diadelphous, in other Leguminosæ (*e.g.* the Pea) where, of the ten stamens, nine are fused

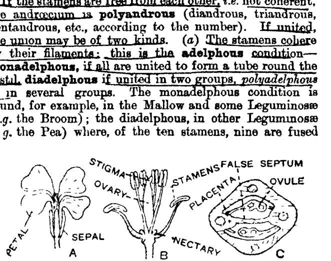


Fig. 128.—Flower of a Crucifer.

A, Entire—cruciform corolla; B, Sepals and petals removed—tetradynamous stamens; C, Transverse section of ovary.

and the tenth is free; the polyadelphous, in the St John's Wort and Orange. (*b*) The stamens cohere by their anthers, the filaments being free. This is characteristic of Compositæ (*e.g.* Daisy, Dandelion, Thistle, etc.), some Solanaceæ (*e.g.* the Bitter-sweet and Potato), etc. It is the **syngenesious** or **synantherous condition** (Fig. 124, A).

Where the stamens in a flower have different lengths, special terms are sometimes applied to the andrœcium. Thus, in the order Cruciferæ (Wall-flower, Stock, etc.) there are four long and two short stamens (Fig. 128, B), and the andrœcium is said to be **tetradynamous**. In Labiatæ, Verbenaceæ, and Scrophulariaceæ (*e.g.* Foxglove), where there are two long and two short stamens, it is **didynamous**. These are the only common orders in which these terms are used.

§ 19. Insertion of the Anthers.—The attachment of the anther to the filament should be noticed (Fig 126). It is *innate* or *basifixed* if the anther is fixed directly on top of the filament; *adnate* if the connective is well marked, and there is no articulation of the filament to the base of the anther, so that the filament seems to run up the back of the anther; *dorsifixed* if the filament is attached to the back of the anther and the anther is immovable; *versatile* if the attachment is similar, but the anther swings on the filament.

§ 20. Dehiscence of the Anthers.—Usually each anther-lobe bursts open (dehisces) by a longitudinal slit between the two pollen-sacs The dehiscence is brought about by the contraction of the reticulately thickened cells of the **fibrous layer,** the inner of the two layers forming the wall of the loculus (Fig 127). According as the anther-lobes face inwards (towards the centre of the flower) or outwards, the anthers or the dehiscence is said to be *introrse* or *extrorse*. The dehiscence may be transverse, as in some Labiatæ, by means of flaps or valves, as in the Laurel, or, as in Heaths, Rhododendron, and Potato, it may be effected by pores at the apices of the anther-lobes.

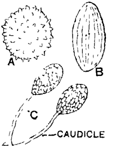


Fig 129 —A, B, POLLEN-GRAINS (HIGHLY MAGNIFIED), C, POLLINIA OF AN ORCHID (p 330).

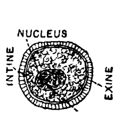


Fig 130 —YOUNG POLLEN-GRAIN OF A LILY (Section)

§ 21. **The pollen,** in most plants, forms a loose, dusty powder, consisting of a large number of minute grains (Fig. 129, A, B). The grains vary much in size, form, and colour in different plants. At first (Fig. 130)

they are unicellular and the wall consists of two membranes or coats. The outer coat, the *exine*, is cuticularised and frequently ornamented with protuberances, spines, etc. The inner coat, the *intine*, is thin and consists of cellulose. In some plants, e.g. Orchids, the pollen-grains are not loose, but aggregated into a single mass called a **pollinium** (Fig 129, c).

Before seed can be produced the pollen-grains must be transferred to the stigma, either of the same flower, or of another flower of the same species.

The development of the pollen-sacs and pollen-grains will be described later.

§ 22 **The Gynæceum or Pistil**, consisting of carpels, forms the inner essential organ of the flower. It is the part of the flower which has been most extensively and completely modified. The student, indeed, finds it difficult at first to realise that it consists of leaf-organs It is necessary, therefore, that he should read very carefully the description which follows, making sure that he fully understands the exact significance of the terms used.

The gynæceum may be **monocarpellary** or **polycarpellary**,* that is, it may consist of one or of several carpels. In the latter case, according to the number, it is bicarpellary, tricarpellary, etc.

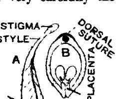


Fig. 131.—The Monocarpellary Pistil.
A, Entire, B, Transverse section of ovary, C, Will indicate method of folding.

§ 23. **The Monocarpellary Pistil** (Fig. 131).—The student must imagine that a single carpellary leaf has been folded on itself so that its margins become coherent along a line known as the *ventral suture*; and, further, that the apex of the leaf has become elongated and slightly swollen at the tip.

* Notice—"poly-" here has not the same significance as in polypetalous, etc.

The hollow basal portion of the folded carpel is the **ovary**, from which the fruit is afterwards developed; it contains a varying number of oval or rounded bodies, the **ovules**, which afterwards develop into seeds. The slender prolongation, of varying length, on top of the ovary is the **style**, which often contains a central cavity communicating with the cavity of the ovary, but may be composed of loose tissue throughout. The apical portion of the style, called the **stigma**, is usually swollen and covered with hairs or glandular papillæ, as we shall see later, it forms the receptive surface for the pollen.

If we examine the ovary, we find that the ovules are *marginal*, *i e* they are developed on the fused margins of the carpel. The fused margins form a longitudinal ridge or cushion of tissue, called the **placenta**, along the ventral suture, on the inner surface of the ovary wall. The dorsal suture (Fig. 131) corresponds to the midrib of the carpel. Seeing that the placenta is on the wall of the ovary, the **placentation** (*i e.* the position or arrangement of placentas in an ovary) is **parietal**. Usually, however, in the *simple* ovary the placentation is simply described as marginal. The monocarpellary pistil is easily recognised by the presence of this single placenta. The pistil of the Leguminosæ (Pea, Bean, etc) is an excellent example.

Although we have asked the student to imagine the formation of the monocarpellary pistil as due to the folding of a carpellary leaf, he must not suppose that this process can be observed during the development of the flower We may suppose, however, that something equivalent to it has occurred during the development or evolution of the higher flowering plants We shall see later that in the Gymnosperms the ovules are not enclosed in an ovary at all, but are borne in most cases on the open carpellary leaves. As a matter of fact, in one plant, a Cycad (*Cycas revoluta*), they are borne on the margins of the carpellary leaf. In the higher flowering plants (the Angiosperms) the ovules are protected by being enclosed in an ovary.

§ 24 **The Polycarpellary Gynæceum.**—Of this there are two conditions, according as the carpels are or are not united with each other. If the carpels are free, *each* forms a simple ovary, style and stigma, like the single carpel of the monocarpellary pistil. This is the **apocarpous** con-

dition (Fig. 117 and cf. the terms *polysepalous*, *polypetalous*, *polyandrous*). Here, while there is a single gynæceum or pistil in the flower, there is a number of simple ovaries. The number indicates the number of carpels. The placentation is marginal. Frequently, only one ovule is developed in each loculus (many Ranunculaceæ and Rosaceæ); if the ovule is attached to the top of the loculus it is *pendulous*; if to the bottom, *ascending*

In the second condition all the carpels are united to form a single *compound* (or polymerous) ovary, and the pistil is **syncarpous** (cf. the terms gamopetalous, gamosepalous, etc.). The union may or may not be complete. If complete, the ovary bears a single style and stigma (Fig. 132, A), and it is only by the internal structure of the ovary that the number of carpels can be determined If incomplete, a number of styles or stigmas are borne on the single ovary (Fig 132, B, C), owing to the apices of the carpels remaining free It is evident that the number of styles or stigmas gives the number of carpels. Thus, in Compositæ (Fig. 124, A) the style is single, but there are two stigmas; hence we know that the pistil is bicarpellary.

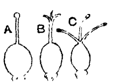


Fig. 132 —THE SYNCARPOUS PISTIL.
(To indicate different degrees of fusion.)

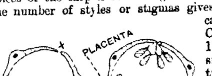


Fig 133 —FORMATION OF THE UNILOCULAR OVARY OF A TRICARPELLARY PISTIL.
X indicates points of fusion (Placentation parietal. Transverse section.)

The structure of the ovary and the placentation in the syncarpous pistil differs in different cases. The following conditions should be carefully noticed :—

(*a*) The carpels simply fuse by their adjacent margins (Fig 133) to form a unilocular ovary. The fused margins

swell up to form placentas bearing ovules. The placentation is marginal and parietal. The number of parietal placentas indicates the number of carpels.

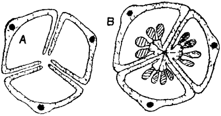


FIG 134.—FORMATION OF A TRILOCULAR OVARY WITH AXILE PLACENTATION (Transverse section)

(*b*) The carpels are folded on themselves before fusing, or we might say that the fused margins run in to the middle of the ovary (Fig 134) Thus a multilocular ovary is formed, and the marginal placentas of all the carpels fuse in the centre to form a central or axile column. The placentation is marginal and axile. The number of loculi, or the number of septa by which the ovary is divided, indicates the number of carpels (except where *false* septa are formed—see below). Sometimes only one ovule is developed in each loculus. It is *suspended* if it comes off from the placenta high up and hangs down in the loculus (Fig. 135); but sometimes there is no distinct axile placenta—the ovule being either *ascending* or *pendulous* (p. 239).



FIG. 135.—VERTICAL SECTION OF UMBELLIFEROUS FLOWER.

In the ovary of the Poppy there is an intermediate condition between (*a*) and (*b*). The septa, which are covered with ovules and are therefore placentas, do not reach the middle of the ovary. The ovary is unilocular, but partially divided. The placentation is parietal

(*c*) The carpels fuse by their adjacent margins and the ovary is unilocular as in (*a*). But the ovules are not developed on the carpellary margins They are borne on a central axis running through the middle of the ovary. The placentation is **free-central.**

In typical cases (Primulaceæ, Fig 125) the central axis is a prolongation of the thalamus into the ovary. The ovules are developed on the axis of the flower, not on the carpels There are, however, a few orders (*e g* Caryophyllaceæ) in which the free-central placenta is derived from an originally axile placentation by the breaking down of the septa

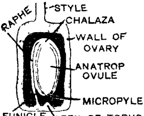


FIG 136 — INFERIOR OVARY OF A COMPOSITE (Longitudinal section)

Basal placentation is a modification of typical free central. Here a single ovule is inserted on the floor of the ovary. It is developed on the thalamus, which, however, is not prolonged as an axis into the ovary (*e g.* Polygonaceæ, Fig 137, and Compositæ, Fig 136)

The ovules are, in rare cases, developed, not on the margins of the carpels, but over the whole inner surface, *e g.* the Flowering Rush (apocarpous) and Water Lily (syncarpous) This is called **superficial placentation.**

§ 25 **True and False Septa.**—*True* septa, or dissepiments, are those which represent the inturned margins of carpellary leaves. Septa formed in any other way, *e.g.* as ingrowths from the surfaces of the carpels, are *false* In the ovary of Cruciferæ (Fig 128, c), for example, the false septum is formed by two membranes, which grow in from the two parietal placentas, and meet and overlap in the centre.

§ 26 **Superior and Inferior Ovaries.**—In all hypogynous and perigynous conditions, the ovary is described as *superior*; in the epigynous condition, as *inferior*. It might seem out of place to describe the ovary as superior, and the calyx inferior, in such a perigynous condition as is shown in Fig 119, D But the student must remember that the ovary here is developed at the *organic* apex of the thalamus, and is free from the calyx-tube.

§ 27 **Structure of Ovule.**—If we examine a typical ovule (Fig 137), we find that it is attached by a slender stalk—the **funiculus**, or **funicle**—to the placenta. The body of the ovule consists of a mass of parenchymatous tissue, called the **nucellus**, and either one or two cellular coats or **integuments**. These integuments arise during development from the base of the nucellus, and completely invest it, except at the apex, where a small canal or passage is left leading down to the apex of the nucellus This passage is called the **micropyle.** In most Gamopetalous Dicotyledons there is only one integument. The base of the nucellus, from which the integuments arise, is called the **chalaza.** The point where the body of the ovule is attached to its stalk, or funicle, is the **hilum** (see p 66)

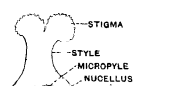


Fig 137—Ovary and Basal Orthotropous Ovule of *Polygonum*) (Longitudinal section)

Towards the micropylar end of the nucellus there is a large, specially developed cell. This is the **embryo-sac.** In the embryo-sac the protoplasm is arranged as in an ordinary parenchymatous cell. There is a lining or parietal layer and protoplasmic strands. Vacuole and cell-sap are present In addition to this, however, several *cells* are present in the embryo-sac, formed, as will afterwards be explained (Chapter XVI), by free cell-formation. At the micropylar end there are three cells without cell-walls constituting the egg-apparatus. The largest one is the **oosphere, ovum,** or **egg-cell**; the two smaller ones are called the **synergidæ,** or **help-cells.** At the other end there are three cells with cell-walls. These are the **antipodal cells.** Embedded in the protoplasm in the middle of the embryo-sac there is a large nucleus, called the **secondary** or **definitive nucleus** of the embryo-sac.

The above gives the general structure of the fully-formed ovule at the time when fertilisation is just about to take place. The development of the ovule will be described later (Chapter XVI).

§ 28. **Forms of Ovule.**—There are several important forms of ovule to be noticed. The typical form is the *straight* or **orthotropous** ovule (Fig 137). Here the ovule is perfectly straight, not curved or bent in any way. The chalaza and hilum lie close together, and the micropyle is at the extreme apex.

In the *inverted* or **anatropous** form (Fig. 138) the body of the ovule has bent over during development, and fused for some distance with the stalk or funicle. This fused portion of the funicle is called the **raphe.** In this form the micropyle and hilum lie close together, and the chalaza is towards the other end.

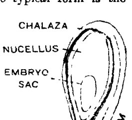


FIG 138 —ANATROPOUS OVULE. (Longitudinal section.)

In the **curved** or **campylotropous** form (Fig 139, B) the body is curved and bent round, so that the micropyle

lies near the funicle; but there is no fusion with the funicle. Hilum, chalaza, and micropyle, all lie close together The **amphitropous** ovule is an intermediate form in which the body of the ovule is straight, but has been twisted round, so that its long axis is at right angles to the funicle (Fig 139, A)

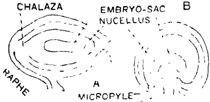


Fig 139.—Forms of Ovule
A, Amphitropous, B, Campylotropous.

Of these forms the anatropous is most frequently met with Examples of the campylotropous ovule are found in many Cruciferæ (Wall-flower, etc) and Leguminosæ (Pea, Bean, Broom, etc) The orthotropous ovule is less frequently found, e g *Polygonum* (Fig 137). The Primulaceæ and some Cruciferae give examples of the amphitropous ovule.

§ 29. **Cohesion and Adhesion.**—The student must be clear as to the meaning of these terms. *Cohesion* is union between members of the same series of floral leaves Thus gamosepalous, polysepalous, polyandrous, syngenesious, apocarpous, syncarpous, are terms signifying cohesion or want of cohesion *Adhesion* means union between members of different series, as when the stamens are epipetalous We have already explained that cohesion or adhesion of parts in the flower is not due to the actual fusion of parts originally separate, but to common basal growth during development

§ 30 **Modification of Floral Structure.**—The *primitive* typical flower, we may suppose, was regular, and showed no cohesion of parts The countless diverse modifications now existing may be ascribed to the operation of various processes of which many examples have been suggested in the foregoing pages

The chief of these are —*abbreviation* of the floral axis; closely connected with this the *displacement* of parts, and the *cohesion* or *adhesion* of parts owing to common basal growth during development, *branching* or *splitting* (chorisis) of parts, as in the inner whorl of stamens in the Cruciferæ, where the two pairs of stamens (Fig. 128, B) are due to splitting of two originally single ones, *reduction* or complete *suppression* of parts, e.g. the reduction of stamens to staminodes, the reduction of petals to nectariferous organs (many Ranunculaceæ), the loss of calyx in many Umbelliferæ and Compositæ, *development of irregularity*, due to hypertrophy of certain parts—this, as will afterwards be explained, is closely connected with the pollination of flowers by insects.

The student should notice examples of these processes. At the same time he should recognise the general principle underlying all this—namely, the more or less perfect adaptation of the flower to the function which it has to carry on in relation to the conditions of its environment

§ 31 **Vertical Sections and Floral Diagrams.**—The general structure and arrangement of parts in a flower may be shown in drawings of longitudinal or vertical sections (Figs. 119, 121, 135), in floral diagrams and floral formulæ.

The **floral diagram** may be described as a ground-plan of the flower showing the relation of the parts to each other and to the mother-axis (Fig. 140). In making a floral diagram the student must clearly distinguish the *antero-posterior* or median, the *lateral*, and the *diagonal* planes (Fig. 141). Cohesion of parts may be indicated by connecting lines (Fig 142, A), but this may be done in the floral formula which should accompany the diagram. The æstivation also may be indicated as in Fig 143 An *empirical* diagram (Fig 142, B) is one showing only the relative positions of the parts actually present. A *theoretical* one indicates, as well, by means of dots, the relative positions of parts which, we may conclude, were originally present, but are now lost (Fig. 142, C).

The student will experience most difficulty in indicating the positions relative to the mother-axis. It will help

him if he remembers that in most Dicotyledons one sepal is *posterior*. An exception is found in the order Leguminosæ (Fig 144), and there are also exceptional cases

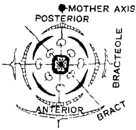


Fig 140 —Floral Diagram of a Regular Tetramerous Flower.

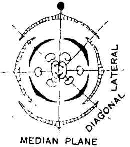


Fig 141 —Floral Diagram of Cruciferæ.

where the posterior sepal has been lost (Fig 142, B, C) Fig 145 shows the characteristic arrangement in typical Monocotyledons

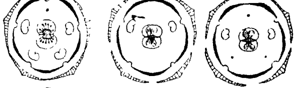


Fig 142 —Floral Diagrams of Scrophulariaceæ.
A, Common form, B, Empirical diagram of Speedwell, C, Theoretical diagram of Speedwell

The **floral formula,** together with the diagram and longitudinal section, enables us to represent all the essential *morphological* features of the flower without a word of description being necessary

The symbols ⊕ and † respectively denote radially and bilaterally symmetrical (zygomorphic) flowers, the direction

of the arrow indicating the plane of symmetry along which the flower can be divided into equal halves. The signs ♂, ♀, ☿ respectively denote staminate, carpellary, and hermaphrodite ("perfect") flowers The letters K, C,

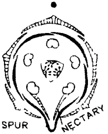


Fig 143 —FLORAL DIAGRAM OF VIOLET

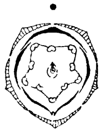


Fig 144 —FLORAL DIAGRAM OF LEGUMINOSÆ. (Monadelphous form)

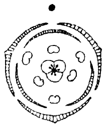


Fig 145 —TYPICAL FLORAL DIAGRAM OF MONOCOTYLEDONS (e g Lily).

and P represent calyx, corolla, and perianth, A and G the andrœcium (stamens) and gynæceum (pistil), and the figure following each letter gives the number of parts in each series. Cohesion is indicated by brackets enclosing the number of parts; a horizontal bracket ⌒ indicates adhesion between the parts of successive whorls; a horizontal line above the number after G means that the ovary is inferior, a line below, that it is superior; the symbol ∞ is used when there are numerous parts in any series.

Thus the floral formula of the Primrose

$$☿\ \oplus\ K(5)\ \overset{\frown}{C(5)\,A}0 + 5\ G(\underline{5})$$

reads—hermaphrodite, radially symmetrical flower, gamosepalous calyx of five sepals, gamopetalous corolla of five petals, andrœcium of five free epipetalous stamens superposed on the petals (antipetalous), syncarpous pistil of five carpels with a superior ovary

The floral formulæ of many common plants are given in Chapter XIII.

[*Directions for the description of flowers are given in the Appendix.*]

CHAPTER X.

THE INFLORESCENCE.

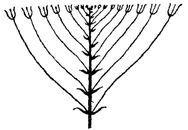
§ 1. **The Inflorescence** is the floral region of the plant as distinguished from the vegetative Its simplest form is the solitary terminal flower. Usually it is a more or less complex branch-system. Inflorescences are best classified according to the type of branching, and the special modifications in each case Probably in all the branching is lateral, and they are either (*a*) *indefinite* or *racemose*, (*b*) *definite* or *cymose*. In the former the growing point has an indefinite power of growth; it never ends in a flower, although the actual number of lateral flowers which it produces may be few or many. In cymose inflorescences the primary axis and the successive daughter axes in turn end in flowers

It is characteristic of racemose inflorescences that the youngest flowers are always found towards the apex, or, where a cluster of flowers is formed, towards the centre (*centripetal*), while, in compact cymose inflorescences, the youngest flowers are towards the outside, *i.e.* away from the centre (*centrifugal*) This is why the terms centripetal and centrifugal are sometimes used for the two kinds of inflorescence.

§ 2 **Simple Racemose Inflorescences.**—Of these we recognise four chief types :—

(*a*) **The typical raceme** (Fig. 118) —Here the mother-axis (peduncle) is elongated, and the flowers are stalked Examples are found in the Peacock-flower, Gold-mohur tree, Mustard, etc.

Similar to this in essential characters is the **corymb,** which may be regarded as a modification of the typical raceme. The mother-axis is relatively shorter, and, owing to the elongation of the lower pedicels, all the flowers come to one level (Fig 146) This is an improvement on the typical raceme, for the close aggregation of flowers renders the whole inflorescence more conspicuous, and there is no need therefore for the individual flowers developing large corollas to attract insects. Good examples are found in many Cruciferæ (*e g.* Candytuft).


FIG 146 —THE CORYMB.

Inflorescences intermediate in character between the corymb and typical raceme are described as corymbose racemes, *e g* the Wall-flower, in which the inflorescence is corymbose when young, but lengthens out when fruiting

(*b*) **The spike** is a racemose inflorescence in which the mother-axis is elongated, and the flowers are *sessile* (Fig. 147), e g. *Sorghum*, *Achyranthes*, and others. By this arrangement small flowers may be aggregated in a cylindrical mass



FIG 147 —A TYPICAL SPIKE

There are one or two special forms of the spike. The **spadix** is a massive fleshy spike, bearing small, usually unisexual flowers. It is protected by a large enveloping leaf, sometimes green, more usually petaloid, known as a *spathe* * The spathe and upper part of the spadix serve to attract insects, and sometimes, as in the Arum Lily (Fig. 148), there is a fly-trap mechanism in connection with the pollination of the flowers The **catkin**

* The spathe is usually called a bract—the term bract being used in the wider sense (see p. 221)

or *amentum* (Fig. 149) is a long, more or less pendulous, deciduous spike, bearing unisexual flowers It is found in many nut-bearing and other trees, *e g* Birch, Hazel, Poplar. The male catkin as a rule dangles loosely in the air so that the pollen, which is protected from rain by the catkin scales, is readily blown out by the wind.

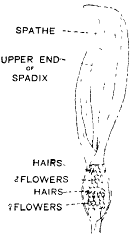


Fig 148 — Spadix of Arum
Part of lower end of spathe removed to expose the flowers.

(*c*) The **umbel** (Fig 150) is a racemose inflorescence in which the flowers are stalked, but, owing to the abbreviation of the mother-axis, are all given off at one level There is an indefinite growing point which throws off a large number of lateral flowers, but does not give rise to an elongated mother-axis We may suppose this to have been derived from the raceme or corymb by compression, all the daughter-axes being brought to one level, just as the flower itself may be described as a compressed shoot,

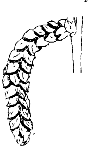


Fig 149 — A Catkin



Fig 150 — The Simple Umbel

in which, owing to the shortening of the internodes, all the whorls of floral leaves lie close together.

(*d*) **The capitulum** (Fig. 151) is a racemose inflorescence in which the flowers are sessile, and crowded together on a reduced or abbreviated mother-axis (peduncle). We may suppose it to have been derived from the spike in the same way as the umbel from the raceme. The mother-axis is called the *disc* or *receptacle*.* It is sometimes flat, more frequently dilated and convex. Examples are found chiefly in the Compositæ (Daisy, Dandelion, etc.). The student must clearly recognise that the heads of the Daisy, Dandelion, etc., are not single flowers, but inflorescences bearing a large number of sessile flowers. The capitulum is invested by a number of small, scaly, overlapping leaves, which are spoken of as barren bracts. The protective investment thus formed is called the **involucre.**

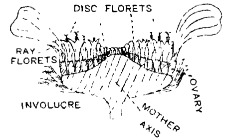


FIG 151.—THE CAPITULUM (Vertical section.)

The massing together of small flowers in the umbel and capitulum has the same biological significance as in the corymb.

§ 3. **Cymose Inflorescence.**—These are either *uniparous, biparous, or multiparous* (see p 80). In the uniparous forms each successive axis ends in a flower after producing one daughter-axis. They may be *helicoid* or *scorpioid*, are *sympodial*, and sometimes resemble typical racemes (see Fig. 47, B, D). Uniparous cymes resembling racemes can be distinguished by the fact that the bracts, if they are

* The term receptacle is ambiguous, being also applied to the thalamus. The student must clearly distinguish the two applications of the term.

present, are on the opposite side of the sympodial axis from the leaves If bracts are not developed they are not easily distinguished

In the *biparous* cyme each axis ends in a flower after producing two daughter-axes. It is also called the **dichasium** or *false dichotomy* (Fig 152) Typical examples are found in many Caryophyllaceæ Sometimes the daughter-axes are not given off at the same level, *e g* some Buttercups, Christmas Rose, etc.

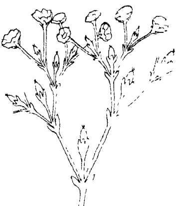


Fig 152 — DICHASIUM OR BIPAROUS CYME

In the *multiparous* cyme, a whorl of daughter-axes is given off before the mother-axis ends in a flower Here a cymose umbel is formed, clearly distinguished from the racemose or typical umbel by the fact that the oldest flower is in the middle.

§ 4 **Compound and Mixed Inflorescences.**—Many inflorescences have not the simple characters above described, and present considerable difficulty to the student In practical work—and it should be remembered that book knowledge is worth little or nothing here—he should begin by carefully recognising the simple forms before proceeding to the analysis of the more complex.

Many inflorescences are **compound**, *e g*. a raceme of racemes, a spike of spikelets (Rye Grass), an umbel of umbels The *panicle* is a compound irregularly branched raceme It is the most primitive type of inflorescence, for it is really the modified upper region of the plant, whereas the simple raceme is more highly differentiated and has become simple by reduction The *compound umbel*

(Fig. 153) is frequently found in the order Umbelliferæ; here the bracts at the base of the chief branches constitute the *involucre*—the smaller bracts at the base of each secondary umbel, the *involucel*. The inflorescence in the Elder is a compound multiparous cyme, in which some of the branches given off are larger than others.

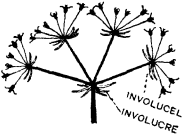


Fig 153 THE COMPOUND UMBEL.

Many inflorescences are **mixed**. We may, for example, have a raceme of spikes, a raceme of capitula, a spike of capitula, a raceme of cymes, etc. The *panicle of spikelets* is a common form in many grasses (*e g.* the Oat); in the Horse Chestnut there is a raceme of short cymes and the inflorescence is called a *thyrsus*. In the Lilac the inflorescence is of the same nature, but the branching is much more copious. Sometimes the name *racemose* or *panicled thyrsoid cyme* is applied to such an inflorescence

§ 5. **Special Forms.**—There are many inflorescences which, owing to abbreviation of axes or special crowding of the flowers, do not so readily yield to careful analysis. In the Hawthorn, for example, the inflorescence might be mistaken for a typical corymb. Examination will show, however, that the lateral axes borne on the main axis are really cymes It is a *corymbose cyme*.

In the cultivated Geranium * and many species of Narcissus the inflorescence, at first sight, appears to be an umbel. But it will be found that the young flowers are not by any means aggregated towards the centre, and that the flowers are arranged in a number of groups. These are really cymose clusters. We may speak of the whole inflorescence as an *umbellate cymose head*. These are found in many

* Which is really a Pelargonium.

plants. In Narcissus the inflorescence is protected by a membranous *spathe*.

In *Leucas*, Tulsi, and many other members of the Labiatæ, the leaves are opposite and decussate, and at each

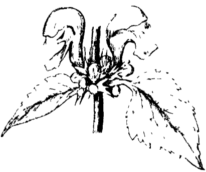


Fig 154 —VERTICILLASTER OF LABIATÆ.

node there seems to be a whorl of flowers These *apparent* whorls are called **verticillasters** (Fig 154) Careful analysis shows that there is in the axil of each leaf an inflorescence which is a dichasium of scorpioid cymes, *i e.* a biparous cyme which passes on either side into a uniparous form by suppression of one of the branches at each branching It is difficult to recognise this because the axes have been reduced and the flowers are sessile. It is easily recognised in many Labiatæ where the flowers have short stalks. In Fig. 155 the axis which ends in flower 1 gives rise to two daughter-axes, 2, ending in flowers Each of these gives rise to an axis, 3, and so on

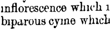


Fig 155 —DIAGRAM INDICATING THE RELATION OF FLOWERS IN HALF OF A VERTICILLASTER

In the Sweet William and some other plants there is a copiously branched biparous cyme, in which the axes are short and all the flowers crowded together. This clustered form is called a *fascicle*.

The **cyathium** (Fig. 156) is a peculiar inflorescence found in *Euphorbia* (the Spurge). There is a cup-shaped involucre the margin of which bears a number of crescent shaped glandular scales. Inside the cup there are a number of stamens; also a gynæceum borne on a stalk. The whole structure looks like a single flower; but each stamen is really a male or staminate flower, and the gynæceum with its stalk is the female or pistillate flower This is borne out by the fact that each stamen is articulated to a stalk and has a scaly bract at its base

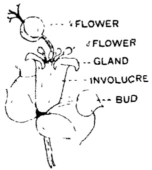


Fig 156 —Cyathium of Euphorbia.

§ 6 **Comparison of Cymose and Racemose Types.**—It seems probable that all cymose inflorescences have been derived from racemose ones by a shortening of the main axis and a delay in the development of the lateral branches, to which the main power of growth is at the same time transferred

The cymose inflorescence is certainly an advance upon the racemose type, for in the former new flowers continually appear on the exposed surface of the inflorescence, while the fruits ripen securely buried among the older parts of the mass of branches The tendency in racemes, on the other hand, is to simultaneous flowering, such as is exhibited more or less perfectly by many umbels and capitula and especially by corymbs In such cases there is an ever-present danger that the short period of flowering may occur at a time when the conditions are not suitable for the production of fertile seed

Racemes such as those of the Wallflower, in which the lower flowers may open months before the apex of the raceme ceases flowering, do not incur this danger, but the exposed position of the young succulent fruits is an obvious disadvantage here and in other Crucifers also Moreover, if the growing point of a young raceme is destroyed, the power of producing flowers may be temporarily lost, whereas the destruction of the apex of a cyme involves the loss of a single flower only, and the lateral axes continue their growth with even greater vigour than before.

CHAPTER XI.

REPRODUCTION AND LIFE-HISTORY OF THE ANGIOSPERM

§ 1 Hitherto we have been dealing chiefly with the individual plant—its structure, nutrition, and growth We have now to see how the plant reproduces its kind and perpetuates the species, for that is the ultimate object of its existence. In connection with the reproductive processes we shall consider the general course of development —in other words, the life-history of the plant.

§ 2. **Vegetative Reproduction** (p 16) —The essential feature in all vegetative reproduction is that the more or less specialised part which is separated off from the vegetative region of the parent *directly* develops into a new plant *resembling the parent* The part thus separated off has different forms in different cases, but in nearly all cases in the higher plants it either consists of a bud, more or less specialised, or bears one or more buds The bud, being either buried in the soil, or in contact with the soil, sends down roots from its base, while above ground it develops into a shoot The development, at first, is dependent on stored food-material.

Copious vegetative reproduction is found amongst the Angiosperms, and it takes many forms. Sometimes specialised buds are developed for this purpose, *e g*. bulbils (p 85), while in many plants, if a shoot happens to be buried in the soil, the ordinary buds in the axils of the leaves send down roots, and develop into shoots which become separated. Vegetative reproduction by means of runners, suckers, tubers, bulbs, corms, rhizomes, etc., has already been referred to in Chapter IV. As a rule, vegetative reproduction does not lead to any very wide distribution of a plant.

§ 3. **Reproduction by Seed.**—This is by far the more important method, tending, as it does, not only to maintain the vigour and vitality of the species, but also to secure its more extended distribution. We shall find that in the formation of the seed a sexual process (p. 16) takes place in the plant, similar in all essential points to that which is found in animals The processes which lead up to the formation of seed and fruit are very complicated, and we must now consider them in detail.

§ 4. **Pollination.**—In order that seed may be produced, the pollen grains must be transferred from the anthers to the stigma. The meaning of this will be explained in what follows. This transference of the pollen-grains is called **pollination.** There may be (*a*) **self-pollination;** or (*b*) **cross-pollination.** In the former, the pollen-grains simply fall, or are transferred in some way, from the anthers to the stigma or stigmas *of the same flower*. In the latter, they are carried in various ways to the stigma or stigmas *of other flowers*, either on the same plant, or on different plants of the same species. As pollination is followed, later, by the process of fertilisation, the terms *self-fertilisation* (**autogamy**) and *cross-fertilisation* (**allogamy**) are often used. The student, however, must carefully distinguish between pollination and fertilisation.

The great majority of Angiosperms have hermaphrodite flowers, and therefore one would perhaps naturally expect, in most cases, to find self-pollination. As a matter of fact, however, cross-pollination is of general occurrence in hermaphrodite flowers, and most of them show obvious adaptations for securing it.

This being so, we must believe that there is some considerable advantage accruing to the species from cross-pollination. The probable explanation has been supplied by numerous experiments in pollination made on plants. It has been found that, when cross-pollination occurs, the resulting seeds either are more numerous, or are heavier, and give rise to stronger offspring than is the case when self-pollination occurs. This is more especially the case when the pollen is transferred, not simply from one flower

to another on the same plant, but from one plant to another. Now, we may correlate this with the fact that in sexual reproduction the offspring inherits characters from both sides. In self-pollination there is simply the mixing of practically similar characters, while in cross-pollination there is a mixing of more or less dissimilar characters. In the latter case useful variations are more likely to arise, and be transmitted, giving the offspring a better chance in the struggle for existence.

Self-pollination, however, is of extremely common occurrence in hermaphrodite flowers, even in many which are evidently well-adapted for cross-pollination, and cases are not uncommon where special arrangements are made for self-pollination. This seems to indicate that, in most plants, *occasional* cross-pollination only is necessary—that it need not be of regular, or even of frequent occurrence.

Cross-pollination may be effected by various agencies. Thus, the pollen may be transferred by means of the wind, water, or animals, and the flowers are said to be **anemophilous, hydrophilous, or zoophilous** respectively. Grasses, Meadow Rue, Nettle, are good examples of anemophilous flowers. Hydrophilous flowers are found in a few water-plants; but most aquatic plants raise their flowers well out of the water and are pollinated by wind or by insects. While we have examples of flowers being pollinated by means of such animals as slugs, snails, humming-birds, etc., the animals thus employed are, in nearly all cases, insects (flies, moths, bees, etc.). Such flowers are said to be **entomophilous**. The great majority of Angiospermous flowers are such. Here we recognise an intimate interrelation existing between the plant and animal kingdoms.

§ 5. **Contrivances and Conditions favouring Cross-pollination.**—There are in flowers many arrangements and mechanisms which can only be interpreted as adaptations for cross-pollination. Usually such arrangements and mechanisms merely give chances in favour of cross-pollination without precluding the possibility of

self-pollination. Sometimes, however, they make self-pollination difficult, or altogether impossible.

In plants with unisexual flowers, of course, cross-pollination is absolutely necessary if seed is to be produced. We have this condition in its extreme form in diœcious plants, *e.g.* the Date. There are a few plants, also, in which cross-pollination must take place because the plants are *self-sterile*, *i.e.* the flower cannot be fertilised by its own pollen; this occurs in some species of Passion-flower, of Lobelia, and of Abutilon. In some plants, again, self-pollination may be rendered unlikely or difficult owing to the relative position of anthers and stigma.

A condition of much more general occurrence is that known as **Dichogamy**. This is a condition in which the anthers and stigma in hermaphrodite flowers come to maturity at different times, and which, when completely developed, entirely prevents self-pollination.

There are two forms of Dichogamy: (*a*) **protandry**, in which the anthers ripen first, so that when the pollen-grains are shed the stigma of the same flower is not ready to receive them, in this case, if the pollen-grains are not to be wasted, they must be transferred to an older flower; (*b*) **protogyny**, in which the stigma ripens first; here the pollen-grains are transferred to a younger flower. Protandrous flowers are much more common than protogynous. Examples of the former are found in Compositæ, Labiatæ, Umbelliferæ, Harebells, Willow-herbs, etc.; of the latter in *Plantago*, many Rushes (*Juncaceæ*), some Palms, Christmas Rose, etc Wind-pollinated flowers are more often protogynous than protandrous, but many are unisexual.

Anemophilous and entomophilous flowers have each special characters of their own, so that as a rule we can distinguish them at a glance. In *anemophilous flowers* the pollen is usually dry and smooth, and is produced in great abundance, as much of it must be wasted; the flowers are small and inconspicuous; there is no honey or perfume; and frequently the stigmas are branched and feathery, to catch the pollen-grains. In many trees which are wind-pollinated the flowers appear in spring before the

leaves, so that the pollen-grains have free access to the flowers. In most herbaceous plants with wind-pollinated flowers, the latter are carried up on a long stalk, well above the leaves, so as to expose them as freely as possible to the wind (*e g* *Plantago*, Docks, Sorrels, etc).

Much greater variety of adaptation is shown by *entomophilous flowers* · As a rule they have large, conspicuous, or highly-coloured corollas, or are arranged in conspicuous inflorescences, they usually secrete honey and give out perfume. The pollen is usually rough and sticky, and is not produced in any great abundance, as the provision for its transference is more perfect. The bright corollas, the perfume and honey serve to attract insects. To understand this, the student must remember that insects do not visit flowers for nothing. They go in search of food. In return for the service rendered by insects the flowers sacrifice part of their nutritive substance in providing food to the insects (honey and pollen), and make a further sacrifice in developing certain structures (corollas) which will attract the insects By instinct insects associate these attractive structures with the presence of a supply of food-material.

A honeyless but otherwise insect-attracting flower is sometimes called a "pollen-flower." Examples are found in Poppies, Dog Rose, Rock-rose, Wood Anemone, Traveller's Joy, St. John's Wort, Gorse, Broom, Meadow Sweet These flowers are visited by insects for pollen.

Many entomophilous flowers are further characterised by the presence of ingenious mechanical devices, which guide and control the movements of the insect and turn them to the best account Thus, in many cases, the corolla is so modified that the insect must alight on the flower or enter it in a special way (*e g* Labiatæ, Leguminosæ); the same result may be attained by the secretion of nectar into special receptacles or spurs (*e g.* in the Violet). Often the insect, on entering a flower, pushes against special processes or outgrowths which move the stamens and bring the anthers in contact with its body (*e.g.* in the Sage); or the stamens may be jerked, and the pollen scattered over the insect's body. Frequently spots or lines of a conspicuous colour are developed on the corolla; these have

been called "honey-guides," as they are believed to afford insects guidance in seeking out the honey.

The general result of all these devices is that the insect receives the pollen on a special part of its body, and when it enters another flower the pollen is deposited on the stigma. In many protandrous flowers this is secured by the style bending over so that the stigma is in the position formerly occupied by the stamens.

A very special, but at the same time very simple, arrangement for making the best use of the insects is the condition known as **heterostyly.** It is seen in many Rubiaceæ. Here there are two types of flower borne on different plants One kind (thrum-eyed) has long stamens (with anthers in the throat of the corolla tube) and a short style, the other (pin-eyed) has a long style and short stamens; thus in the two types the positions of anthers and stigma are simply reversed Evidently pollination will be most readily effected by transference between these two forms (legitimate pollination) and not between two flowers of the same form (illegitimate pollination), and experiment has proved that the best seed is produced when this is the case. In the Rubiaceæ there are two kinds of flower, this is the dimorphic form of heterostyly. In the Purple Loosestrife (*Lythrum*) and in *Oxalis* there are three, i e. flowers with long, short, and medium styles; this is the trimorphic form. *Woodfordia floribunda* (Lythraceæ) also shows heterostyly.

§ 6 **Insects that visit Flowers.**—The chief flower-visiting insects are beetles (Coleoptera), flies (Diptera), bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera) In connection with the pollination of flowers, the important differences to be noticed between these insects are the size of the body, the length of the tongue (proboscis), the time of year at which each kind is most plentiful, and their habits—*e g.* whether they collect pollen or honey or both, whether they fly by day or in the evening. By carefully studying the structure of a flower, and noting such points as the time of flowering, the order in which the anthers and stigmas mature, the relative positions of anthers and stigmas in the open flower

and any changes in position that may occur, we can often tell what kind of insect is capable of effecting cross-pollination, and whether or not self-pollination is possible

Most flies and beetles have very short tongues, usually less than 3 mm. long. Most of the larger and longer-tongued flies, e g Gad-flies, "Cleggs," and Horseflies (which are blood suckers) do not visit flowers, but there are some, chiefly Hover-flies and Bee flies, with tongues sometimes as long as 12 mm, which are regular flower-visitors

Flowers may be arranged in various biological groups or classes according to their adaptations for insect-visitation :—

(1) **Flowers adapted for Short-tongued Insects.**—These may be (a) flowers in which the honey is freely exposed on the surface, e g Ivy, Umbelliferæ, Golden Saxifrage, etc ; (b) flowers with a very short tube, e g. Moschatel, Bedstraw, Enchanter's Nightshade, (c) shallow open flowers such as Stonecrop and Saxifrages Such flowers are visited by the shorter-tongued beetles and flies.

(2) **Flowers with partially-concealed Honey.**—This group includes flowers in which the honey can be reached only by insects with tongues at least 3 mm in length, and which are therefore visited by the longer-tongued beetles and flies, as well as by insects of higher type. The honey may be slightly concealed by the stamens, e g Buttercup and Stitchwort, by the erect stiff sepals, as in the smaller Cruciferæ; by the formation of a shallow calyx-tube, as in many Rosaceæ (e g Strawberry), by a short corolla tube, e g the shorter-tubed Compositæ, Guelder Rose, etc.

(3) **Flowers with fully-concealed Honey**—This type of flower differs only in degree from the last. Here the honey can only be reached by insects having tongues about 6 mm long, including the longest-tongued flies (chiefly hover flies), the shorter tongued bees, and wasps The concealment of the honey is effected by a further deepening of the flower, owing to the formation of a calyx-tube, to the calyx being gamosepalous or the corolla gamopetalous, or to other causes Examples of these medium-tubed flowers are seen in the Blackberry, Currants, Gooseberry, Willow herb, Geranium, Speedwell, etc. The Figwort, Snowberry, and Barberry are examples of flowers largely visited by wasps

(4) **Long-tubed Flowers.**—When the flower-tube becomes longer, all the shorter-tongued insects are more or less completely excluded, and the flower is adapted for, and chiefly visited by, the larger bees, butterflies, and moths Many flowers belonging to the Lily, Daffodil, and Iris families of Monocotyledons, in which the perianth nearly always forms a long tube, come under this type Flowers like those of Papilionaceæ, Snapdragon, and Toadflax can only be opened by large bees, and only the longest tongued bees can reach the honey in such flowers as Monkshood and Larkspur.

Humble- and hive-bees have the most perfect mechanism (the "pollen-baskets" on the hind-legs) for collecting pollen to mix with honey and feed their broods. Humble-bees have longer tongues than hive-bees, and are particularly skilful in finding the way to well-concealed honey.

Blue, purple, and red colours are often associated with flowers visited by bees (especially blue and purple) and butterflies (especially red), while flowers visited by other insects are usually white, yellow, or variegated; but there are far too many exceptions to allow of a general rule

(5) **Butterfly- and Moth-Flowers.**—When the flower-tube (or at any rate the level of the honey) is more than about 12 mm. (about half an inch) deep, the honey is beyond the reach of bees, though they may visit the flower for pollen, or the humble-bee may bite through the tube (calyx or corolla) and thus rob the flower of its honey Good examples of butterfly-flowers are seen in the Pinks, Red Campion, Corn-cockle, but butterflies also visit many flowers which are adapted for bees, *most* butterflies and moths having tongues of about the same length as, or a little longer than, those of bees.

Some moths, however, have far longer tongues (30 mm. or more in British species), which are (as in butterflies) carried coiled up in a spiral under the head when flying. These moths can reach honey when it is at the bottom of a very long tube, as in the Honeysuckle, which is visited chiefly by the night-flying Privet Hawk-moth, and the White Convolvulus, which is pollinated by another species of Hawk-moth (*Sphinx convolvuli*, tongue 80 mm long), and rarely sets seed in England owing to the rarity of this moth. Other flowers pollinated by night-flying moths are the White Campion (*Lychnis vespertina*), Evening Primrose, Tobacco Plant, and Privet Moth-pollinated flowers are white or pale-coloured, sweetly scented, and open in the evening, usually remaining closed and almost scentless during the day.

§ 7. Examples of Floral Mechanism.—(*a*) In the **Garden Pansy** (Fig. 157) the anthers of the five stamens are firmly joined by hairs on their edges, and the two anterior stamens bear processes, functioning as nectar glands, which pass down into the spur of the anterior petal A space or chamber ("pollen-box") is enclosed above the ovary, at the base of the style, by the five membranous scales borne on top of the anthers The stigma, which projects beyond the anther-scales, is dilated and hollow. It has a tuft of hairs on each side, and below there is an opening into it, the lower edge of which is protected by a lip or flap (the "scraper").

The flowers are not *erect*, but hang down, and hence the pollen, which is shed on the inner faces of the anthers, and is dry and loose, not sticky as in most entomophilous flowers, falls into the "pollen-box," from which it can escape only through the opening

between the scales of the two anterior anthers The stigma is protected, and self-pollination thus prevented, by the "scraper."

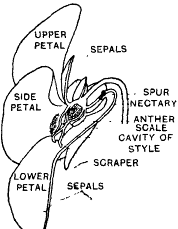


Fig 157 —Longitudinal Section of Flower of Garden Pansy

The flowers are pollinated by long-tongued bees (and butterflies). When the insect enters the flower, pollen obtained from another flower may be deposited on the stigma, and cross pollination thus effected. Pushing down into the spur of the anterior petal to reach the honey, the insect receives a supply of pollen which has escaped from the "pollen-box" The "scraper" prevents this pollen being deposited on the stigma as the insect retires

The visits of desirable insects are encouraged by the conspicuously coloured centre of the flower, and by the honey-guides on the lateral and spur-petals The entrance of small undesirable visitors is hindered by the hairs on the lateral petals and on the sides of the stigma, by the hairs lining the entrance and cavity of the spur, and by the length of the spur itself.

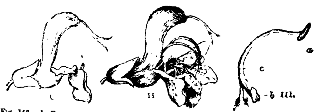


Fig 158 —I, Flower of Sage from side ; II, with Humble bee extracting nectar, and the Anthers rubbing against its back, III, S'hole Stamen

(*b*) In the **Sage** (*Salvia*), one of the Labiate Family, an interesting mechanism is found (Fig 158) The corolla is bilabiate The conspicuous lower lip attracts insects, and acts as a landing place

The arched upper lip protects the stamens and style. There are only two stamens, the other two, characteristic of the Labiate Family, being represented in the Sage by staminodes.

The two stamens have a peculiar structure. Each has a short filament, jointed to a long curved connective (Fig. 158, III. *c*). In the lower types of *Salvia* each end of the connective bears a half-anther, but in the higher types (*e g* the Garden Sage) the lower end of the connective is barren and flattened (Fig. 158, III. *b*), and the upper part of the connective is longer than the lower, the whole forming a delicate lever.

A bee on entering the flower pushes against the *united* lower ends of the two connectives in seeking for the honey, and causes the curved connectives to swing on the filaments as on hinges, so that the two fertile anther-lobes (*a*) come down and strike the bee's back, dusting it with pollen. As the bee retires, the stamens return to their former place under the corolla-hood.

The flowers are protandrous As the flower gets older the style bends down, and the stigma is first touched by a bee entering the flower

§ 8 **Special Arrangements for Self-Pollination.**—In studying floral mechanisms we are too apt to forget that self-pollination occurs regularly in most flowers where it is not precluded by diœcism, complete dichogamy, or self-sterility, that it is rarely *much* inferior to cross-pollination in its results, and that it is always better than *no* pollination

Many annual plants cannot afford to undertake the risks and sacrifices attendant on cross-pollination and are commonly self-pollinated (*e g.* Groundsel, Chickweed). They have small flowers, often without honey or smell, and are either **homogamous**, that is, their anthers and stigmas mature at the same time, or so slightly dichogamous that self-pollination is secure

Even in flowers evidently adapted for cross-pollination there is commonly the possibility of self-pollination as a last resort. Many of them are distinctly dichogamous, but not completely so, there being usually a short period during which self-pollination becomes possible. To effect this there are sometimes special contrivances such as the curling back of the stigmas to reach the pollen (*e.g.* Compositæ, Campanulaceæ).

A very special adaptation for self-pollination is the production of **cleistogamous flowers.** These are closed

flowers produced late in the year by certain plants which had previously produced entomophilous flowers, *e.g.* the Sweet Violet, the Wood Sorrel, *Lamium amplexicaule* (one of the Dead-nettles), etc In these plants the ordinary entomophilous flowers frequently fail to produce seed The cleistogamous flower is small and inconspicuous. The calyx never opens, and the stamens and pistil are developed in a closed case

In the Sweet Violet the self-pollinating cleistogamic flowers have five very small petals and five stamens, but in the Dog Violet there are only two stamens The anthers produce few pollen-grains, and do not open; the grains germinate inside the anther, and the pollen-tubes (see § 10) grow through the anther-wall and the style to reach the ovules The formation of these flowers is partly dependent on shade, they are always shaded by the leaves of the plant itself If a plant is kept in feeble light, it will usually produce only those cleistogamic flowers. They are probably to be regarded as derived from flowers of the ordinary type which have undergone reduction owing to diminished nutrition.

§ 9. **Protection of Pollen against Rain.**—Pollen-grains, like seeds, are much less resistant to extremes of temperature and to drying when once they have been moistened and have begun in consequence to germinate Pollen may be protected from rain in various ways In some flowers, especially those whose pollen is exposed to rain when the flower opens, the pollen grains are not readily wetted, having a covering of wax or of spines, etc.

Many flowers protect the pollen by their horizontal or drooping position, *e g* Heaths, Bluebell, Lily of the Valley, Violet. In some cases the flower closes up at night or in bad weather, *e g* Wood Sorrel, Tulip, Crocus, Lesser Celandine, Scarlet Pimpernel, and the same kind of closing is effected in the flower-heads of many Composites by the movement of the flowers and bracts. In the Iris the large petaloid stigmas cover the stamens, and in many flowers the stamens are protected by a hood formed by the sepals or petals, or by both.

§ 10 **Germination of the Pollen Grain. Processes leading up to and ending in Fertilisation.**—At first the pollen grain is unicellular (Fig. 130), but later, even

before it leaves the anther, its nucleus and protoplasm divide to form two cells (Fig. 159, A). One of these, the **generative cell**, is small and lies freely in the protoplasm of the larger or **vegetative cell**. Either before or after pollination it divides again into two **male cells** or **gametes** (see p 16). There are no cell-walls between these cells Germination and further development take place on the stigma, which secretes a sugary nutritive fluid.

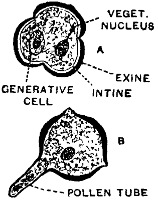


Fig 159 —GERMINATION OF POLLEN-GRAIN

The **vegetative cell** bursts the exine at a point where it is thin and grows out into a very slender **pollen-tube** (Fig 159, B). The pollen-tube grows down through the tissue of stigma and style and finally enters the ovary Its development and growth are at first stimulated and directed by chemical substances contained in the stigma This is an example of **chemotaxis** or sensitiveness to chemical stimuli (p. 213). Its growth through the tissue of stigma and style is effected by ferment action and closely resembles that of the hypha of a fungus

After entering the ovary the pollen-tube is guided in various ways towards an ovule, which it enters usually by the micropyle It pierces the apex of the nucellus and comes in contact with the embryo-sac near to the oosphere and synergidæ The male gametes together with the nucleus of the vegetative cell have by this time passed down to the apex of the pollen-tube. *One male gamete only* is concerned in the actual process of fertilisation. It passes from the pollen tube into the embryo-sac and fuses with the oosphere. The synergidæ assist in the process, hence their name synergidæ or "help-cells" (Gr. σνν, with, ἐργον, work) They contain little protoplasm, but plenty

of sap which is absorbed by the pollen-tube when it has reached the surface of the sac. This causes the tip of the pollen-tube to swell and burst, thus setting the male gametes free.

The fusion of the protoplasm and nucleus of the male gamete with those of the oosphere constitutes fertilisation in the strict sense. It is evidently a sexual union similar to that which occurs in animals. The oosphere is the female cell or gamete. During the process the vegetative nucleus is disorganised. The fertilised oosphere forms a cellulose wall and is then called the **oospore** (p. 45).

The fate of the second male gamete was, until recently, unknown. It has now been shown, in many plants, that it passes to the middle of the embryo-sac and fuses with the secondary nucleus. The resulting nucleus is called the *endosperm-nucleus*. The significance of this process, which resembles fertilisation, and which, together with the actual fertilisation of the oosphere, constitutes what has been called **"double fertilisation,"** is considered in § 12.

In a very few Dicotyledons, e.g. the Hazel and Birch, the pollen-tube does not enter the ovule by the micropyle, but by piercing the chalaza or base of the ovule. This is known as **chalazogamic** fertilisation as distinguished from the usual or **porogamic** method. It has no systematic importance, as it occurs in plants which are not closely related to each other.

§ 11. **Development of the Embryo.**—The stimulus of fertilisation induces changes in the embryo-sac and ovary, and leads to the development of the seed and fruit. The embryo is developed from the oospore. After fertilisation the synergidæ disappear.

The development of the embryo in the Shepherd's Purse (*Capsella bursa-pastoris*) may be taken as fairly typical of Dicotyledons generally. The oospore first of all divides into two cells, an upper and a lower (Fig. 160). The upper cell, which becomes attached to the micropylar end of the embryo-sac, further divides by a series of divisions parallel to the first and gives rise to a row or filament of cells called the **suspensor.** The lower cell is attached to the end of this and divides by three walls

at right angles into eight cells (octants). Four of these are posterior (next the suspensor), four anterior. This little mass of tissue is called the **embryonal mass.**

As the embryonal mass increases in size the various parts of the embryo are gradually differentiated. The

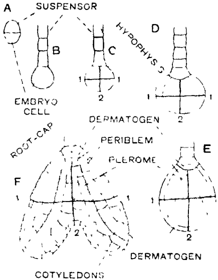


FIG 160 – DEVELOPMENT OF DICOTYLEDONOUS EMBRYO (*Capsella bursa pastoris*, THE SHEPHERD'S PURSE).

A, First division of oospore Only two of the octant-walls (1, 2) can be shown.

terminal plumule and the two cotyledons are derived from the four anterior octants, the hypocotyl from the posterior octants, the growing point of the radicle—in other words, the primary root—is derived from the terminal cell of the suspensor, called the **hypophysis cell.** The marking out of plerome, etc, can be readily followed in Fig 160.

In Monocotyledons also the first division of the oospore is into upper and lower cells; but the course of

development differs in different groups, and there is no monocotyledonous plant in which the development of the embryo can be regarded as typical of Monocotyledons generally. In some cases no suspensor is formed and the whole of the embryo is developed from the embryonal cell. In other cases there is a filamentous suspensor which takes part to a greater or less extent in the formation of the embryo. This is the characteristic mode of development in monocotyledonous aquatic plants of which *Alisma plantago* may be taken as the type (Fig. 161). In the Lily family, which may be taken as more characteristic of Monocotyledons generally, the suspensor is massive and the greater part of the embryo is developed from the embryonal mass.

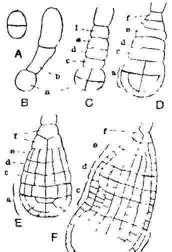


Fig. 161.—DEVELOPMENT OF MONOCOTYLEDONOUS EMBRYO (*Alisma*).

a is the Embryonal Cell (in B) forming the embryonal mass (in C, D, E, F); it gives rise to the cotyledon. *c*, *d*, *e*, *f* are formed by division of *b*, the terminal cell of suspensor. *c* gives growing-point of stem; *d*, *e* give hypocotyl; *f*, the growing point of root.

The chief point to notice in the development of the monocotyledonous embryo is that, except in a very few cases, the cotyledon is a *terminal structure*, and the plumule arises as a lateral outgrowth.

In some plants, *e.g.* Orchids and various parasitic plants, the embryo remains in a rudimentary state till the seed is formed.

§ 12. **Development of the Endosperm.**—While the segmentation of the oospore and the development of the embryo are taking place other changes are proceeding in

the embryo-sac. The endosperm-nucleus begins rapid karyokinetic division, and produces a large number of small nuclei embedded in the protoplasm of the embryo-sac. The protoplasm aggregates round these nuclei to form protoplasts (p. 20) and finally cell-walls are laid down between them Thus by a process of free cell-formation (p. 44), starting from the endosperm-nucleus, a tissue is formed in the embryo-sac. The cells of this tissue become laden with food-material (starch, oil, aleurone grains, etc) built up from soluble compounds which diffuse into them from the placenta. The nutritive tissue thus formed *in* the embryo-sac is the **endosperm.**

The significance of the fusion of the second male gamete with the secondary nucleus of the embryo-sac ("double fertilisation," p. 268) is not understood. By some it is regarded as an act of fertilisation, in which case the endosperm would be an undifferentiated embryo devoted to supplying the actual embryo with food At present, however, we may accept provisionally the other and more probable view, that the fusion merely provides the necessary stimulus to the development of the endosperm tissue.

In a few plants, more especially when the embryo sac is large, the endosperm is not produced by free cell-formation, but by ordinary cell-division of the embryo-sac, *i e* the secondary nucleus divides into two, and then a wall is laid down dividing the embryo-sac into two cells, in each of which the process is repeated.

§ 13. **Apogamy and Parthenogenesis.**—In a few cases amongst Flowering Plants (*e g.* in species of *Thalictrum, Alchemilla*, and various Composites) the oosphere or egg cell may develop into an embryo, *although unfertilised* This phenomenon, in which an embryo is developed in spite of the omission of the sexual process, is called *apogamy*. Sometimes in lower plants the embryo is developed by a purely vegetative process. When, as in the flowering plants mentioned, it is developed from an unfertilised egg-cell the phenomenon is called parthenogenetic apogamy or parthenogenesis.

§ 14. **Adventitious Embryos — Polyembryony.** — In some plants a number of embryos may be formed in one ovule, and be found in the seed which is produced This phenomenon is known as *polyembryony*. It may be due to the presence of more than one embryo sac in the same ovule, or of more than one egg-cell in the embryo-sac. As a rule, however, the embryos arise by purely

vegetative budding from the cells of the nucellus (*e.g.* in Orange and Lemon), or in rare cases from the antipodal cells. Embryos formed in this way are called adventitious embryos and are examples of purely vegetative apogamy in Flowering Plants

§ 15. **Formation of Seed and Fruit.**—The embryo-sac with its developing contents increases in size, and the nucellus is gradually crushed and disorganised, and finally disappears. The integument or integuments of the ovule become dry and firm, and form the seed-coat surrounding and protecting the embryo and endosperm. The ovule has now developed into the seed.

In all seeds at an early stage endosperm is present. If the embryo remains small, and the endosperm persists, the fully-formed seed is *albuminous* (most Monocotyledons and many Dicotyledons). In many Dicotyledons, however, and in a few Monocotyledons, the cotyledons of the embryo absorb the endosperm tissue while the seed is ripening, in this case the endosperm disappears, and the embryo is large. These are *exalbuminous* seeds.

In a very few cases the nucellus is not completely disorganised, but, like the endosperm tissue, becomes laden with food-material. The nutritive tissue thus formed *outside* the embryo-sac, and therefore quite distinct from the endosperm, is called **perisperm** (*e.g.* Water Lily and Pepper).

It does not follow that all the ovules whose egg-cells are fertilised form fully developed seeds. In many cases there is a struggle for dominance amongst the developing seeds in an ovary owing to a limited supply of food-material or other causes. Not unfrequently only one ovule comes to maturity. Thus in the Oak and Beech the ovary is trilocular, with two ovules in each loculus, but the fruit is unilocular and one-seeded.

The **seed**, then, is the highly specialised reproductive structure which is formed in Flowering Plants by developmental changes induced in the ovule by the stimulus of fertilisation. But the student has now to notice that these induced or stimulated developments are not confined to the ovule, but extend to other parts. Processes of *secondary growth* are set up in the ovary and the neighbouring parts

of the flower. The entire result of these changes constitutes the **fruit** in the wide sense of the term.

The function of the fruit is to protect the seed, and to secure its proper dispersal at the right time.

§ 16 **The Suspensor.**—It is only occasionally that the suspensor acts as an absorbing organ. Its function is simply to push the embryo down into the endosperm Sometimes, however, when the suspensor is massive, it sends out processes which pierce the nucellus and integuments, bury themselves in the placenta, and take up food-material (some Orchids).

§ 17 **Development of the New Plant.**—A period of rest, previous to germination, usually follows the complete development of the seed This period may be short or long. Many seeds can retain their vitality for many years, but if this period is indefinitely prolonged, the vitality is, sooner or later, lost. This explains the sudden appearance of weeds on land which has been reclaimed and brought under cultivation

Thus the development of the oospore into the adult plant takes place in two stages—one inside the seed, leading to the formation of an embryo, the other when germination takes place, and the embryo develops into the adult plant (see p 213).

§ 18. **Aril and Caruncle.**—Sometimes *after fertilisation* an additional investment is formed on the seed called the *aril.* It may be developed from either the funicle or the micropyle, and is usually fleshy, but may have other forms In the Spindle-tree it is fleshy and micropylar in origin; in the Willow and Poplar it is hairy and funicular. The mace of the nutmeg is an aril developed from both micropyle and funicle. Smaller growths on the seed are called *caruncles*, e g. the Pansy, in which the caruncle is formed at the hilum, the Castor-oil (Fig. 38) and Spurge, where it is formed at the micropyle; the tuft of hairs on the seed of the Willow-herb is also of this nature. Most botanists apply the term aril to *all* growths or investments formed on the seed-coat after fertilisation.

CHAPTER XII.

FRUITS AND SEEDS.

§ 1 **The fruit** of the Angiosperm in the wide sense is the entire result of secondary growth induced in the ovary and neighbouring parts of the flower by the stimulus of fertilisation It usually consists simply of the ripened ovary, but in many cases other parts of the flower take a share in the formation of the fruit, e g the thalamus, or the perianth-leaves The wall of the ovary becomes the **pericarp** or fruit-wall, which may either remain soft and fleshy, or become dry and hard

Botanists have distinguished *true fruits*, formed from the ovary alone, from *false fruits* (*pseudocarps*), in the formation of which other parts of the flower take a part No importance can be attached to this distinction It would lead, for example, to the view that all fruits formed from inferior ovaries are false fruits, seeing that in the inferior ovary the carpels are adherent to the thalamus or calyx-tube. The really important thing in connection with the study of fruits is to recognise that the manifold peculiarities of form and structure which they exhibit are to be interpreted as due to the diversity of ways in which they have been adapted to carry on the functions of seed-protection and seed-dispersal.

§ 2 **Classification of Fruits.**—Fruits may be **simple, aggregate,** or **composite.** A *simple fruit* is one which is formed from a *single* flower in which the pistil is monocarpellary or syncarpous, *e g* the pod of the Pea, the capsule of the Poppy. An *aggregate fruit* is one which is formed from a *single* flower in which the gynæceum is apocarpous Here each carpel (or rather ovary) gives rise to a fruitlet, and the fruit therefore consists of an aggregation of fruitlets. A *composite fruit*, on the other hand, is formed from an *inflorescence*, not from a single flower.

Here all the flowers increase in size, become aggregated together, and form a single mass. These composite fruits are called *syncarps*.

The **Simple Fruits** are further subdivided into **dry** and **succulent** according as the pericarp is dry and firm or more or less fleshy and juicy. The *dry simple* fruits are either **achenial, capsular,** or **schizocarpic;** the *succulent simple* fruits may be **drupaceous, baccate,** or **pomes.** The *aggregate fruits* are collections of one or other of these simple forms. The *syncarps* have peculiarities which distinctly mark them off from these others.

It should be noticed that there is no sharp distinction between dry and succulent fruits. There are examples of fleshy capsules and dry drupes.

§ 3. **Achenial Fruits.**—Achenial fruits may be defined as *dry, indehiscent, one-seeded* fruits. The term indehiscent means that the pericarp does not naturally burst open to allow the seed to escape. The pericarp and testa are both ruptured when the embryo begins to develop at germination. The chief types of achenial fruits are.—

(*a*) The **achene,** in which the pericarp is membranous or leathery. It is formed from a superior ovary, and pericarp and testa are free from each other. Examples are found in the Polygonaceæ (Docks and Sorrels). Many aggregate fruits consist of collections of achenes.

(*b*) The **cypsela** (Figs. 35, 162 A). This differs from the achene only in being developed from an inferior ovary. It is the characteristic fruit of the Compositæ (Sunflower, Daisy, etc.). In many cases it is crowned by a persistent hairy *pappus* (p. 228) which serves to disseminate the fruits (*e.g.* Dandelion, Thistle, Groundsel, etc.).

(*c*) The **caryopsis** (Figs. 39, 162 C). This is simply an achene in which the pericarp and testa are fused together. It is the characteristic fruit of Grasses (Oat, Maize, Barley, etc.). In many cases the fruit or "grain" is invested by the persistent bract and bracteole (*e.g.* the Oat).

(*d*) The **samara,** or *winged* achene. Here the pericarp has developed a membrane or wing which plays an

important part in the dispersal of the fruit, e g. the Maple (*Acer*) (Fig. 167, B) and Elm (*Ulmus*) (Fig 162, B).

(*e*) The **nut**, in which the pericarp is hard and woody, forming a shell. The term is usually applied to all large or hard-coated achenes. Typical examples are found in the Hazel, Oak, Beech, Sweet Chestnut. In these examples the nuts are invested by a hard or membranous structure called the **cupule**, derived from the fusion of bracteoles developed beneath the flower Sometimes the cupule encloses one nut, sometimes several. The cup or cupule

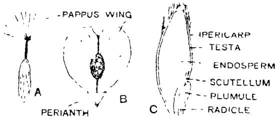


Fig 162 —ACHENIAL FRUITS.

A, Cypsela with pappus, B, Samara of Elm, C Caryopsis of Oat. (C, Longitudinal section—bract and bracteole removed)

of the acorn, the membranous "husk" of the hazel-nut, are well known In the Sweet Chestnut two nuts are enclosed in a spiny cupule, and in the Beech there are usually two triangular nuts enclosed in a cupule which is almost closed and also slightly spiny.

The student must be careful to distinguish these cupules from the capsules presently to be described. He should also notice that many structures, popularly called nuts because they have a hard shell, are not really nuts Thus the "brazil-nut" is a seed (derived from a capsular fruit) The walnut is part of a drupaceous fruit (p 281).

§ 4. **Capsular Fruits.**—These are *dry, dehiscent, many-seeded* fruits The term dehiscent means that the fruits break open naturally to allow the seeds to escape. There are different kinds of capsular fruits.

(*a*) The **follicle** is formed from the ovary of a single carpel. It splits open along one side only, usually the ventral suture (p 237). There is no common example of the simple follicle, but many aggregate fruits consist of follicles (Fig 163).

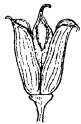


Fig. 163 — Collection (Etærio) of Follicles of Monkshood

(*b*) The **legume** or *pod* (Fig. 88, B) is formed from the ovary of a monocarpellary pistil. It differs from the follicle in dehiscing along both dorsal and ventral sutures. It is the characteristic fruit of the Leguminosæ (Pea, Bean, etc).

(*c*) The **siliqua** is a characteristic fruit of the Cruciferæ, *e g* Wall-flower and Stock It is developed from the ovary of a bicarpellary pistil, in which there are two parietal placentas and a *false* septum stretching between them, so that the ovary is bilocular It is a long, cylindrical fruit, and, in dehiscing, the two walls of the

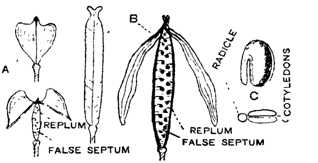


Fig 164 — Fruit and Embryo of Cruciferæ.
A, Silicula, B, Siliqua, C, *One* form of embryo, entire and in section. A and B show the dehiscence.

loculi break away from the two placentas and false septum, and hang freely suspended from the apex of the fruit (Fig. 164, B). Thus the two placentas are left behind, forming a two-ribbed framework called **the replum, across**

which the false septum stretches. The seeds are, of course, exposed on this structure.

(*d*) The **silicula** (Fig 164, A) is simply a short, flat form of siliqua (*e g* Shepherd's Purse, Candytuft, and other Crucifers).

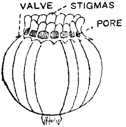


Fig 165 —Capsule of Poppy (Porous dehiscence)

(*e*) The **capsule** includes all other forms of capsular fruits. Capsules are formed from polycarpellary, syncarpous pistils, and may be unilocular or multilocular. Occasionally they are not dry, but more or less fleshy, *e g.* in Horse Chestnut, Balsam, and Wood Sorrel

Various modes of dehiscence are met with. In *porous dehiscence* the seeds escape through little holes or pores in the wall of the capsule, either at the apex (*e g* Poppy, Fig 165) or at the base (*e g* Campanula). The capsule of the Stitchwort and other Caryophyllaceæ splits about half-way down into twice as many teeth as there are carpels (*dehiscence by teeth*) In the Pimpernel and *Plantago* there is transverse dehiscence, leading to the separation of a lid from the top of the capsule Such a capsule is called a

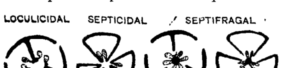


Fig 166 —Dehiscence of Multilocular Capsules. (Diagrammatic transverse sections)

pyxidium. Usually, however, capsules open longitudinally, either along the midribs of the carpels (dorsal sutures) as in Willow-herb and Bluebell, or (more rarely) along the partitions between the chambers of the ovary, as in Foxglove and St John's Wort.

In *multilocular capsules*, with axile placentation, the dehiscence is *loculicidal* (Fig 166) if the slits run down the middle of the carpels (*i.e.* open into the loculi), the *septa and placentas* breaking away in the middle (Iris); *septicidal*, if the slits run down the middle of the septa, the placentas separating in the middle (Rhododendron); *septifragal*, if the slits appear as in loculicidal or septicidal dehiscence but the septa break and the placentas and seeds are left in the middle (*Datura*, the Thorn-apple).

§ 5. **Schizocarpic Fruits (Schizocarps).**—These are dry, many-seeded fruits, which, as they ripen, *split up* into a number of one-seeded and usually indehiscent parts resembling achenes and called **mericarps.** The best known forms are.—

(*a*) **The lomentum.**—This is found in some Leguminosæ (*e g. Hedysarum*, the French Honeysuckle, Fig 167, A) and some Crucifers (*e.g* the Radish), in which the fruit (pod or siliqua) splits *transversely* into one-seeded pieces More strictly the fruit is described as a lomentaceous pod or siliqua, as the case may be.

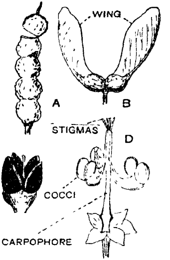


Fig 167 —SCHIZOCARPIC FRUITS
A, Lomentum ; B, Double samara of Maple , C, Carcerulus , D, Regma of Geranium

(*b*) **The cremocarp** (Fig. 168, A, B) —This is the characteristic fruit of the Umbelliferæ. It is developed from a bicarpellary pistil with a bilocular, inferior ovary in each loculus of which there is a single suspended ovule (Fig. 135). As it ripens the cremocarp splits *longitudinally* (between the two loculi) into two mericarps, which remain for some time attached to a prolongation of the axis called the *carpophore*. Each

mericarp contains a seed. These mericarps are *popularly* called seeds, *e g.* the caraway "seed" (Fig. 168, c).

(*c*) **The carcerulus** (Fig 167, c).—This is the characteristic fruit of the orders Labiatæ and Boraginaceæ. In these orders the fruit is formed from a bicarpellary pistil with a *superior* ovary which becomes quadrilocular owing to the formation of two false septa. As the fruit ripens the four mericarps separate from each other towards the middle In the carcerulus of the Mallow the *superior* ovary of the polycarpellary pistil splits into a large number of mericarps.

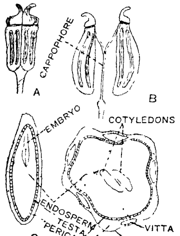


Fig 168 —FRUIT AND SEED OF UMBELLIFERÆ.

A, B, The Cremocarp; C, Longitudinal and transverse sections of a mericarp of the Caraway

(*d*) **The regma** (Fig 167, D) —This is a schizocarp which breaks up into one-seeded *dehiscent* parts, which are not called mericarps, but *cocci*, *e.g.* Geranium and Castor-oil. In the Geranium the pistil is formed of five carpels fused round a long carpophore The five styles of the carpels are also adherent to the carpophore When ripe the cocci break away and remain suspended by their styles from the apex of the carpophore.

(*e*) **The double samara.**—This is the fruit of the Sycamore and Maple (Figs 41, 167 B). Sometimes it consists of three or four samaras instead of two.

§ 6 **Drupes ("Stone" fruits).**—A **simple drupe,** *e g.* Mango, Plum, Apricot, etc, is formed from a monocarpellary pistil with a superior ovary. The pericarp shows

three regions:—(a) the *epicarp* or outer skin, (b) the *mesocarp* or middle fleshy region, and (c) the *endocarp*, the hard inner part, forming the "stone," which encloses and protects the seed. Usually there is only one seed.

The drupe of the Almond has a velvety skin and rather tough mesocarp, which splits along one side; the shell (endocarp) has sometimes two seeds inside it.

Drupes may, however, be syncarpous, in which case each chamber of the ovary may form a distinct stone. The so-called "berries" of Holly, Dogwood, and Elder are really *compound drupes* of this kind. (The walnut and coco-"nut" also are drupes formed from syncarpous pistils.)

The thin mesocarp of the walnut peels off during ripening, and allows the "stone," enclosing a single seed, to escape. The cartilaginous partitions passing in between the cotyledons (which are covered by the testa) are ingrowths from the endocarp

In the coco-nut the mesocarp (removed before exportation) is fibrous Hence the fruit has been called a "fibrous drupe" The shell is the endocarp; the edible substance is the endosperm; and the brown layer covering it the testa A minute monocotyledonous embryo is embedded in the endosperm at one end (below one of the three pits at the broader end of the "nut"). There is a space in the middle of the endosperm filled with sap (so-called "milk"), owing to the fact that the endosperm could not fill the whole of the large embryo-sac.

§ 7. **Baccate Fruits, or Berries.**—These are succulent fruits in which the succulent mass is more or less pulpy, and the seeds, which are usually hard, are embedded in the pulp The berry differs from the drupe essentially in the fact that there is no stony endocarp, although epicarp, mesocarp, and endocarp may be differentiated. Baccate fruits may be derived from inferior ovaries (*e g* Currant, Gooseberry, Pomegranate, Melon, Cucumber), or from superior (*e g.* Grape, Orange).

The *orange* is a multilocular superior berry with axile placentation; the outer glandular skin is the epicarp, the underlying white substance the mesocarp, and the inner

membrane lining the loculi the endocarp. The juice is secreted by a large number of multicellular hairs developed from the walls of the loculi

In the Gooseberry and Pomegranate the pulp, or edible portion of the berry, is derived largely (Gooseberry) or entirely (Pomegranate) from the outer coats of the seeds.

The *date* is recognised as a *berry* and *not a drupe* by the fact that the "stone" is not endocarp but seed (Fig 44) The outer skin of the date is the epicarp; the sticky mass underneath, the mesocarp Surrounding the stone is a thin membranous endocarp The banana is a berry from which, through over-cultivation, the seeds have disappeared

§ 8 **The Pome.**—This is the fruit found in the Apple, Pear, and some other Rosaceæ We may take the Apple as an example In the flower of the Apple there are five imperfectly fused carpels enclosed in a hollow cup-like thalamus (calyx-tube) This is an extreme form of perigyny As development proceeds, however, the carpels become adherent to the calyx-tube so as to produce a practically epigynous condition The whole fused mass forms the pome The outer skin and the fleshy part of the apple are formed from the thalamus The cartilaginous central part (core) is derived mainly from the carpels and is therefore the pericarp containing the seeds. The terms epicarp, mesocarp, and endocarp should not be used for these three regions of the fruit.

In the Hawthorn there may be one or several carpels, and they become stony When there is only one the pome of the Hawthorn closely resembles a drupe Examination, however, would show the remains of the sepals, etc., at the apex of the fruit. These, of course, are not found in the drupe

§ 9 **Aggregate Fruits.**—The aggregates of simple fruitlets are called "**etærios.**" There may be etærios of achenes, follicles, or drupes.

(*a*) A typical *etærio of achenes* is found in the Buttercup (Fig. 117). There the achenes are all grouped together on a slender prolongation of the thalamus In the Hedge Clematis (Traveller's Joy) the etærio of achenes presents a feathery appearance because the styles are persistent and become hairy. The fruit of the Strawberry is an etærio of achenes scattered over the surface of an enlarged fleshy thalamus The achenes here are popularly called seeds. The hip of the Wild Rose consists of an etærio of achenes enclosed in a persistent hollow thalamus or calyx-tube (see Fig 119, E). An interesting comparison can be made between this fruit and the pome.

(*b*) *Etærios of follicles* (Fig. 163) are found in some Ranunculaceæ (*e g* Monkshood, Larkspur, Christmas Rose) and a few Rosaceæ. They will present no difficulty.

(*c*) *Etærios of drupes* —Examples are found in the Blackberry (Bramble) and Raspberry The little drupes, derived from the separate carpels, are inserted on a fleshy, conical thalamus

§ 10. **Composite Fruits.**—These are not numerous, the best examples are the fruits of the *Fig*, *Pineapple*, *Mulberry*, and *Hop*.

(*a*) **The Fig.**—Here the inflorescence is a peculiar hollow, pear-shaped form of capitulum, the flowers being developed inside (Fig. 169, A) The female flowers produce little fruits (achenes), popularly regarded as seeds. The composite fruit formed from this inflorescence is called a **syconus.**

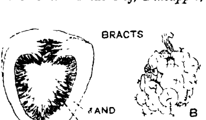


Fig 169 —Composite Fruits.
A, Syconus of Fig (cut vertically), B, Sorosis of Mulberry.

(*b*) **Pineapple** and **Mulberry.**—Here the composite fruit is called a **sorosis.** It is formed from a spike. In the *Pineapple* the fleshy **axis** and **the flowers all fuse**

together The areas on the surface of the fruit represent the flowers. Seeds are rarely formed. Above the flowers the axis produces a number of leaves forming the "crown." In the *Mulberry* (Fig 169, B) the perianths in the female spike become fleshy, and enclose the true fruits. The whole composite fruit resembles closely the fruit of the Blackberry. They must be carefully distinguished. The fruit of the Blackberry is an etærio of drupes developed from the apocarpous pistil *of a single flower*.

(*c*) The **Hop.**—Here the composite fruit is formed from an inflorescence consisting of an axis bearing a number of membranous scales. On the upper surface of each scale, at its base, are two female flowers The fruit is called a **strobilus.** The true fruits are achenes.

§ 11 There are some fruits which it is difficult to classify. For example, the Ivy "berry" is a fleshy fruit containing several seeds, these are not enclosed in a stony endocarp, but there is a firm investment round each The fruit, to some extent, resembles a drupe, and may be called a drupaceous berry.

§ 12 **Dispersal of Seeds and Fruits.**—It is manifestly of advantage to the species that the seeds should be carried some distance from the parent plant. It gives the young seedlings a better chance in the struggle for existence, for they are saved, to a large extent, from the competition with each other in the matter of food, light, etc, which would naturally arise if they were crowded together round the parent. Arrangements for dispersal have an immense importance, also, in connection with the study of the distribution of plants over the earth's surface.

The means of dispersal adopted by different plants vary widely, and are frequently such as to secure the almost ubiquitous distribution of some plants. The four commonest agencies by which dispersal is secured are :—(1) **Wind,** (2) **water,** (3) **animals,** (4) **explosive** or **ejection mechanisms** in the fruit itself.

§ 13 **Dispersal by wind** is facilitated by many different arrangements and contrivances which are to be regarded as adaptations for this mode of dispersal. It should be

noticed that it is only in the case of *dehiscent* fruits that adaptive mechanisms are borne by the seed, closed fruits and the segments (mericarps) of splitting fruits are themselves distributed, and possess contrivances for dispersal.

(*a*) The seeds of some plants (*e g.* Orchids) are so small and light that when they are set free from the fruits they are freely blown about by the wind.

(*b*) "*Censer mechanism.*"—When the seeds are larger and heavier the fruit frequently opens in such a way that the seeds can only escape a few at a time, and are jerked out when the plant sways in a high wind. This censer mechanism is seen in follicles (*e g* Monkshood), in many capsules which dehisce by pores (Poppy and Campanula), or by teeth (Campions, Stitchworts, Primrose), and in some capsules with longitudinal dehiscence (Lily and Iris); it is also seen in the fruiting heads of some Composites where the achenes have no pappus, *e.g.* Sunflower.

(*c*) As an aid to wind-dispersal, seeds are frequently flattened (*e g.* Wallflower), as also are the fruit-segments of some Umbelliferæ, and the achenes of Buttercups and some Compositæ

(*d*) "*Parachute mechanisms.*"—Special structures of the nature of wing-like or hairy outgrowths are frequently present which enable the seeds or fruits to be more readily carried by the wind. The **plumed seeds** of *Calotropis*, *Nerium*, Willow-herb, and Bog Asphodel have hairy outgrowths of the nature of arils. **Winged seeds** are found in Yellow Rattle, *Deutzia*, and *Bignonia*. Good examples of **winged fruits** are seen in *Pterocarpus*, *Pongamia*, and Birch, and the "keys" of Maple and Sycamore. In the Lime, the stalk bearing the cluster of nuts hangs down, and the large bract attached to it acts as a kite or aeroplane. In Docks the fruit is covered by the calyx which bears three wings. In the Teasel there is a funnel-shaped wing formed from persistent bracts. As examples of **plumed fruits** we have the achenes with persistent hairy styles of Clematis and Pasque-flower, and the pappus-crowned cypselas of many Composites. It is interesting to notice in what various ways these structures, which are adaptations to wind-dispersal, are developed.

Dispersal by wind involves a greater loss of seeds than dispersal by animals, for the latter usually frequent fertile localities where the seeds have a chance of germinating, whereas wind-dispersed seeds may fall upon sterile or unsuitable localities, or may be carried out to sea. It is for this reason that winged and hairy seeds are usually absent from the plants of the seashore. Hence also arises the fact that wind-dispersed seeds are usually produced in relatively greater abundance than those dispersed by animals.

§ 14. **Dispersal by Water** is uncommon and occurs chiefly in water-plants In most aquatic plants the fruits are developed under water, and are usually achenes, nuts, or splitting fruits which do not float. In a few, however, *e g* Alder and Water Lily, the seeds are enabled to float to a distance by being provided with a spongy covering (aril) containing air See pp 482, 484

§ 15 **Dispersal by Animals.**—Seeds and fruits may be dispersed by animals, either by adhering to them or by being eaten by them.

In the former case certain structures, of the nature of hooked spines, are developed by which the fruits become attached to the fur or wool of passing animals These adhesive structures are usually outgrowths of the fruit and not of the seed. Examples are found in Love-grass, *Xanthium*, Enchanter's Nightshade, some Umbelliferæ (*e g* Sanicle, Carrot, Chervil). In Avens the persistent styles are hooked In Agrimony the hooks are developed on the receptacle of the flower The flower-heads of Teasel and Burdock have hooked bracts so that a passing animal may catch the plant and drag it forward, the rebound causing the fruits to be jerked out, or, in Burdock, whole burs (fruit-heads) may thus catch on to the animal and be carried off. In the Bur-marigold (*Bidens*) each achene has a pappus of two or three stiff bristles covered with small downward pointing prickles.

Succulent fruits, *e g* drupes, berries, pomes, etc, are eaten

by animals The succulent character is an adaptation to this mode of dispersal. The seeds are protected either by a resistant testa (berries) or a pericarp (*e g.* Strawberry, Wild Rose), or by the seed being enclosed in a strong endocarp (drupes). In many cases the seed can pass through the animal's body without being injured, and if deposited in suitable soil may succeed in germinating. Very often, however, the hard part of the fruit is never swallowed, but allowed to fall to the ground after the soft part has been pecked; for the animals concerned in this mode of dispersal are usually birds whose gizzards may crush small seeds and destroy them

Here again it is interesting to notice from what various parts the succulent mass may be developed—*e g.* ovary-wall in drupes, thalamus in pomes, Strawberry, and Wild Rose, perianth in Mulberry, the aril in some seeds (*e g.* in the Spindle-tree).

§ 16 **Explosive Fruits.**—Some fruits show active movements by which the seeds are scattered or flung out suddenly. These movements often depend upon extreme turgidity in some part of the fruit, *e g* in Squirting Cucumber and Balsams, or of the seed itself. In some Balsams the fleshy capsules have swollen and stretched walls, so that a slight disturbance causes the capsule to burst and the seeds are thrown a few feet away

In some dry fruits the ejecting mechanism depends upon tensions set up by the drying of the fruit-wall. In the Pansy and Violet the capsule splits longitudinally into three concave valves, which by their contraction flick out the smooth, slippery seeds to a considerable distance In the Geranium the styles, by which the carpels remain attached to the carpophore (Fig 167, D), suddenly curl upwards and outwards so as to throw out the seeds. The ripe pods of Gorse, Broom, Lupin, etc, suddenly burst open, the two valves becoming twisted and the seeds scattered.

The seeds of Wood Sorrel have a fleshy aril, which is very elastic. When the capsule opens the aril suddenly turns inside out and jerks the seeds away.

§ 17 **Occasional Dispersal.**—Seeds and fruits may chance to be dispersed in other ways. Many, which are adapted to other modes of dispersal, float when they happen to fall into water, and may be carried a considerable distance in this way. Many also are carried on floating timber and in the mud adhering to the feet of water birds. Various seeds and nuts carried away for food by squirrels or other animals may not be used. Here also we must include the dispersal of seeds and fruits by the agency of man. These *occasional* means of dispersal must be distinguished from the regular modes ***to which plants have adapted themselves***.

CHAPTER XIII.

CLASSIFICATION OF ANGIOSPERMS: NATURAL ORDERS

§ 1 **The Object of Classification** is to arrange plants in a natural scheme, expressing as nearly as possible the affinities or relationships which exist between them owing to descent or evolution from common ancestors There are many difficulties in the way of this and a really natural scheme can never be more than an ideal to be aimed at Any scheme adopted is only an expression of our views concerning these "blood relationships" although, as our knowledge grows by further research, the scheme will become more and more a true reflection of the affinities of plants

§ 2 **Variety, Species, Genus, etc.**—A group or assemblage of plants which resemble each other so closely that we could easily imagine them to be derived from the same parents constitutes a *species* The individuals of a species resemble each other in just those characters which are constantly handed down from parent to offspring Thus all Raspberry plants are included in the species *Rubus idæus*

There is always, however, a certain amount of **variation** among the offspring of plants They present minute individual differences In most cases, within the limits of a species, the variation exhibited is *continuous* or *fluctuating*, i e the varying forms are connected by a continuous series of intermediate forms Sometimes, however, it is discontinuous, i e we find on examining a large number of individuals in a species that they group themselves in two or more sets, races, or **varieties**, which are

hardly connected, if at all, by intermediate forms. There are, for example, two varieties of the common Meadow Buttercup (*Ranunculus acris*): in one the stem is densely hairy at the base, and the segments of the radical leaves overlap each other, in the other variety the stem is only slightly hairy, and the leaf-segments do not overlap.

Varieties differ from each other in small and *variable* characters, chiefly affecting the vegetative organs, but sometimes in floral or seed characters of slight importance, e.g. shape and colour of petals. Species differ from each other in more important and more *constant* characters of the vegetative or floral organs.

Species which resemble each other more or less closely, while each possesses the constant characters which mark it off as a species, are grouped together to form a **genus.** The Banyan and Pipul are such species, together with others they form the genus *Ficus*. We name a plant by giving its generic and specific names. *Ficus benghalensis* is the Banyan, *Ficus religiosa* the Pipul. The differences between genera are more pronounced, important, and constant than those between species.

Similarly, according to wider or more general resemblances, related genera are grouped together into **Natural Orders,** Natural Orders into **Cohorts,** Cohorts into *Series*, and so on to *Sub-Classes*, *Classes*, *Divisions*, and finally *Groups* or *Sub-Kingdoms*. Many of these terms, however, are used arbitrarily. Even the application of the terms *Species* and *Genus* is not definitely fixed.

There are many species which, though variable, have no distinct varieties—that is, they show continuous but not discontinuous variation. A species may have many or few varieties, a genus many or few species, and an order many or few genera. In fact, some genera have only one species, i.e. a species may be so distinct from other plants that it is raised to the rank of a genus. Similarly, a single genus may be regarded as forming an order by itself.

§ 3. **Characters used in Classification.**—The general rule is that *the less any part of the plant is concerned with special habits the more important is it for classification.* For instance, the vegetative organs (roots, stems, leaves) are

of little value in characterising the larger groups, because they are on the whole more liable to variation and modification than are the flowers and fruits, though some vegetative characters (*e g* the alternate or opposite arrangement, and the veining of the leaves) are less liable to modification than others, and can be used in classification.

Of the floral characters the most generally useful is cohesion (*e g.* the polypetalous or gamopetalous condition of the corolla, the apocarpous or syncarpous condition of the pistil); but other characters, such as adhesion, form of receptacle (hypogynous, perigynous, and epigynous conditions), symmetry, number of parts in a whorl, placentation, etc, are also used, as are also the characters of the fruit and seed, *e g* number of cotyledons, form of embryo, presence or absence of endosperm.

§ 4. **Classification of Angiosperms.**—The two main divisions of the Phanerogams or Flowering Plants are the **Angiosperms** and the **Gymnosperms** (see p. 5). The Angiosperms are divided into the two classes **Dicotyledons** and **Monocotyledons**, the distinguishing characters of which have been fully dealt with.

There are two sub-classes of Dicotyledons —(1) the **Archichlamydeæ**, or Lower Dicotyledons, in which the petals are either free or wanting, (2) the **Sympetalæ**, or Higher Dicotyledons, in which the corolla is gamopetalous In both sub-classes the Natural Orders are arranged in a series of Cohorts, beginning with the most primitive and ending with the most highly specialised. The monocotyledonous orders are arranged similarly

This arrangement is based on the classification of Engler and Prantl In Bentham and Hooker's classification, which is followed in British Floras, the Dicotyledons are divided into Polypetalæ, Gamopetalæ, and Apetalæ. Many of the plants included in the Apetalæ, however, are not primitively apetalous (monochlamydeous or achlamydeous), but are reduced forms showing in other respects distinct affinities to polypetalous orders. The inclusion of apetalous and polypetalous forms in a single sub-class is undoubtedly a more natural arrangement.

In beginning the study of classification the student should not trouble himself with any particular general scheme, but should simply aim at making himself acquainted with a number of the commoner Natural Orders This is best done by a careful study and comparison of well-known plants representative of each order.

I DICOTYLEDONS Embryo with two cotyledons; stem with open bundles, usually in one ring; leaf net-veined, flowers with parts in twos, fours, or fives, rarely in threes

A ARCHICHLAMYDEÆ Perianth either absent, or in one whorl, or, if in two whorls, the parts of the inner whorl (petals) free, sometimes one whorl is missing owing to suppression, and *occasionally the corolla is gamopetalous*

B SYMPETALÆ Perianth in two whorls; corolla, with few exceptions, gamopetalous; stamens twice as many

as the petals, or as many, or reduced to 4 or 2, epipetalous except in Ericaceæ and Campanulaceæ

Ericaceæ (p. 342)	Scrophulariaceæ (p 349)
Myrsinaceæ (p 343).	Acanthaceæ (p 352).
Apocynaceæ (p 344).	Rubiaceæ (p 354).
Convolvulaceæ (p. 344).	Cucurbitaceæ (p 355).
Labiatæ (p. 345)	Compositæ (p. 357).
Solanaceæ (p 348).	

II MONOCOTYLEDONS. Embryo with one cotyledon; stem with closed bundles, "scattered" in cross-section; leaves generally parallel-veined, flowers with parts in threes.

Gramineæ (p 362)	Amaryllidaceæ (p 374).
Palmæ (p. 366).	Iridaceæ (p. 376)
Araceæ (p 371).	Musaceæ (p. 378).
Commelinaceæ (p 372)	Orchidaceæ (p 379).
Liliaceæ (p. 373)	

ARCHICHLAMYDEÆ.

§ 5. **Cohort Fagales** (Cupuliferæ).

Distinguishing characters:—Flowers mono- or a-chlamydeous, unisexual, monœcious, borne in catkins. Pistil bi- or tri-carpellary. Fruit dry, indehiscent and one-seeded, a nut or nutlet, frequently invested by a cupule formed by enlarged persistent bracteoles; seed exalbuminous.

This is a group of great interest widely distributed in temperate regions, and nearly all of the genera occur in the Himalaya. It consists of trees and shrubs with simple alternate, stipulate leaves. Two orders are now generally recognised under the cohort—the Betulaceæ and the Fagaceæ. The Himalayan trees belonging to the Betulaceæ are the Birch (*Betula bhojpatra*), on the bark of which many of the ancient Sanskrit manuscripts were written, the Alder (*Alnus*), the Hazel (*Corylus*),

and the Hornbeam (*Carpinus*), and to the Fagaceæ the Oak (*Quercus*), and the Sweet Chestnut (*Castanea*, often separated as a genus *Castanopsis*).

The **inflorescences** are called catkins (p 249) The female catkins are not pendulous. The *typical* **catkin** consists of an elongated pendulous axis bearing numerous spirally arranged scales (bracts) in the axil of each of which are three flowers representing a sessile or reduced dichasium The terminal (middle) flower has two lateral bracteoles, and in the axils of these (as bracts) arise the two lateral flowers, which also may have bracteoles Thus there are typically three flowers and six bracteoles in the axil of each bract (Fig 170). From this it is at once evident that the catkins characteristic of the order are not really simple pendulous spikes (see p. 249).

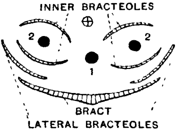


FIG 170 —TYPICAL FLORAL DIAGRAM OF CUPULIFERÆ.

Showing arrangement of bracteoles and flowers 1 = middle flower, 2, 2 = lateral flowers.

The typical form, however, is departed from, more or less, in the various genera. There may be more than three flowers. Sometimes only the middle flower or only the two lateral flowers are present, and some or even all of the bracteoles may be absent The whole inflorescence is, in some cases, reduced to a cluster of flowers The various modifications described below should be carefully studied The female catkins persist till the fruits are ripe, or even longer as in the Alder

The **flowers** are unisexual, monœcious, and borne (with rare exceptions—*e g* sometimes in Chestnut) in different catkins They are anemophilous and, in correlation with this, they frequently come out before the leaves (Hazel and Alder), or just when the leaves are unfolding (Birch and Oak) A **perianth** is sometimes present, and occasionally well developed, when present it is epigynous.

The **stamens** are two, four, or more; sometimes they are split or forked (Figs 173 c, 175). The **gynæceum** is bicarpellary (Betulaceæ), or tricarpellary (Fagaceæ), syncarpous; the *ovary*, at the time of fertilisation, bi- or tri-locular, inferior, *ovules*, one (Betulaceæ) or two (Fagaceæ) in each loculus, anatropous and usually pendulous.

The **fruit** is dry, indehiscent, one-seeded—a nut or nutlet In the Birch it has a membranous wing and is a samara (Fig 173, B). The fruits may be liberated from the coherent bract and bracteoles (Alder and Birch), or these may enclose one or more fruits as a cupule (membranous in Hazel and Hornbeam, woody in Oak). The seed is exalbuminous (Fig 178).

The following notes indicate the special characters of the various genera —



Fig 171.—Birch
Twig showing male and female catkins

Birch (Figs 171-173).—The male catkins appear in autumn at the ends of the shoots and are pendulous; the female catkins are borne on short lateral branches which are developed in spring and are erect. Flowering takes place in April or May In both catkins each bract has three flowers. Only the two lateral bracteoles are present. Each male flower has a small perianth usually two-lobed, and two stamens the filaments of which are so deeply split that there appear to be four stamens. The female flower has no perianth The pistil is bicarpellary and has two styles. The fruits are samaras. Bract and bracteoles become fused owing to continued basal growth. The three-lobed scale which they form falls off at fruiting, but does not invest the fruits.

Alder.—The male catkins are elongated; the female small and somewhat ovoid. Both appear in autumn, and are more or less

erect. Flowering takes place in March or April. Each bract of the male catkin has three flowers, but in the female only the lateral flowers are developed. There are four bracteoles—the two lateral

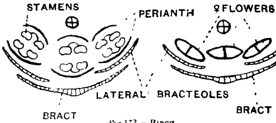


Fig 172.—BIRCH

Diagrams showing arrangement of bracteoles and flowers in male and female catkins.

bracteoles and one to each lateral flower on the side next the bract. The ♂ flower has a four-lobed perianth and four stamens opposite the lobes The ♀ flower resembles that of the Birch The female catkins including the hard five lobed scales formed from the bracts, and bracteoles remain on the tree after the fruits are set free The fruits are not winged (nutlets).

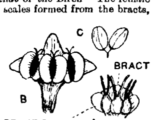


Fig. 173.—BIRCH.

A, Female flowers in axil of bract, B, Fruiting scale, with three samaras, C, Stamen from male flower

Hazel (Figs 174-178).—The catkins appear in autumn The pendulous male catkins are borne 1-3 together on a short axillary shoot The female are solitary, axillary, and are not distinguishable from foliage buds till February or March when flowering takes place and the crimson styles protrude at the top In the male only the median flower and the lateral bracteoles are developed in each scale The flower has four deeply split stamens and there is no perianth In the female catkin the lower scales are sterile; in the upper fertile scales *all* the bracteoles, but only the lateral flowers, are present. Each female flower has a minute, toothed, greenish perianth on the top of the ovary; there are two styles The two bracteoles of each flower with one of the lateral bracteoles fuse, owing to continued basal growth, to form an involucre which develops into the membranous cupule (husk—Fig. 177).

Hornbeam.—The flowers are similar to those of the Hazel, but in the male catkins there are no bracteoles and the male flower has 4 10 split stamens The cupule is large and trilobed (Fig. 179).

Oak (Fig 180).—The catkins appear in the spring, the male in the axils of bud scales, the female in the axils of foliage leaves

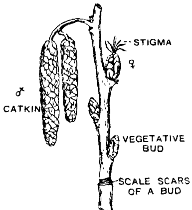


Fig. 174.—MALE AND FEMALE INFLORESCENCES OF THE HAZEL.

Flowering occurs in April or May. The male catkin here is simply a long slender and pendulous spike, the flowers being borne singly in the axils of the bracts. They represent the median flowers and there are no bracteoles. Each (Fig. 180, c) consists of a perianth of a varying number of bract-like segments (4-7) and as many or more stamens (frequently 10). A rudimentary ovary may be present.

The female catkin contains only 2 or 3 flowers which may be in a cluster (*Quercus Robur, var. sessiliflora*) or may be separated by the elongation of the peduncle (*Q. Robur, var. pedunculata*). They are borne in the axils of bracts and represent the median flowers (in some allied species all three flowers are present). Each has an epigynous 3-8 toothed perianth and is surrounded by a number of imbricate scales forming an involucre which afterwards develops into the acorn cup (cupule). The involucre is regarded as representing the four bracteoles of the lateral flowers. The ovary is trilocular, and each loculus has two pendulous anatropous ovules, but only one loculus and one ovule develop. The fruit (acorn) is a nut seated in a cup-shaped cupule. *Quercus Ilex* is the Holly Oak; *Q. Suber*, the Cork Oak.

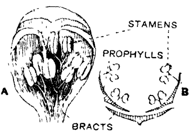


Fig 175.—HAZEL.
A, Male Flower, B, Diagram of same.
(Prophylls = bracteoles)

Chestnut.—The catkins are axillary, and bract and bracteoles are all present. There are usually seven male flowers in the axil of

the bract owing to the bracteoles of the lateral flowers also having flowers. The female bracts bear three flowers and the cupule is

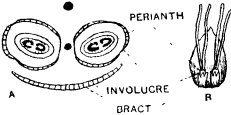


Fig 176.—FEMALE FLOWERS OF HAZEL.
A, Diagram showing bract, bracteoles (involucre) and flowers, B, Bract and flowers.



Fig 177.—TWO HAZEL NUTS INVESTED BY CUPULES.

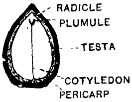


Fig 178.—LONGITUDINAL SECTION OF HAZEL NUT

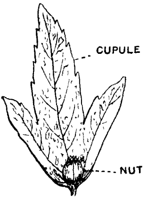


Fig 179.—FRUIT OF HORNBEAM.

formed by the four bracteoles of the lateral flowers The mature cupule is spiny It contains three nuts and separates into four

valves. Frequently catkins are found bearing staminate flowers above and pistillate flowers below.

The Cupuliferæ, Salicaceæ, and other orders (*e.g.* Juglandaceæ, the Walnut order) are sometimes combined

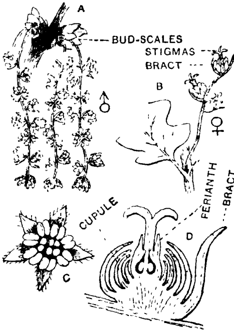


Fig. 180. *Quercus Robur*, VAR. PEDUNCULATA. A, Male; B, Female inflorescences; C, Male flower; D, Female flower in section.

under the cohort **Amentales** (= Amentaceæ or Amentiferæ), the group of catkin-bearing plants.

The early appearance of the Cupuliferæ in time, as shown by fossils, indicates that they are an archaic group of plants. They diverged from the main Angiosperm stem at an early period, and our modern types have survived

because, having the habit of trees, they to a large extent escaped competition with more progressive types *

Some believe that the floral characters—the unisexual flowers, the absence or rudimentary character of the perianth, etc—are primitive, and consider that the chalazogamic fertilisation, which is characteristic of the Betulaceæ, gives further evidence of this. We have seen, however, that there is reason to believe that the early Angiospermous flowers were hermaphrodite (p. 411) Hence it is probable that the simple floral characters of the Cupuliferæ are not primitive, but due to reduction. In this connection the occurrence of rudimentary pistils in the male flowers of the Fagaceæ is interesting

Most, if not all of the Cupuliferæ, have mycorhizæ, which are ectotrophic (ectophytic), *i.e* the mycelial threads do not penetrate the cells of the root.

NOTE —The name Cupuliferæ is now often restricted to the Fagaceæ (*i e.* Cupuliferæ = Fagaceæ).

§ 6. Urticaceæ.

Distinguishing characters·—Mostly herbs or undershrubs, without latex, and with flowers in cymes usually much condensed, unisexual, regular. P4 or 5, free or united, sepaloid, stamens the same, bent down inwards in bud, opposite the perianth leaves, ovary superior, unilocular with one ovule; fruit an achene

This order, as defined by Engler, consists largely of herbs or undershrubs, but in the older classification that was chiefly used in England till a few years ago, it also included many trees, most of which are now separated in the order Moraceæ, described below. There is no latex in the Urticaceæ, and their leaves are alternate or opposite, and stipulate. Many have stinging hairs—stiff hairs, turgid with an acid sap, and with a peculiar glassy point to the cell, which is easily broken off, allowing the poison to escape (see p. 60). Some of the Laporteas, known to English

* Progressive and up-to-date orders, *e g.* Compositæ, are largely or entirely represented by herbaceous forms.

people as fever- or devil-nettles, and *Girardinia heterophylla*, the Nilgiri Nettle (Bichhú Búti) sting very severely.

The **inflorescences** are usually axillary cymes which may be panicled in appearance or more or less clustered (glomerules). The **flowers** (Figs 181-183) are regular, monochlamydeous, unisexual or, occasionally, hermaphrodite

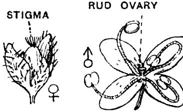


Fig 181 Fig 182. URTICACEÆ: MALE AND FEMALE FLOWERS.

Perianth of four or five leaves, poly- or gamo-phyllous, green, inferior, persistent **Stamens** equal to the perianth segments and opposite to them The stamens are at first folded inwards and downwards in the flower, but when ripe, or when moved, they spring up violently and give out a little cloud of pollen (an adaptation for pollen protection and wind pollination). **Pistil** monocarpellary; *ovary* superior, unilocular, with one basal, orthotropous ovule Stigmas tufted and often sessile The male flowers have a rudimentary pistil The **fruit** is an achene enclosed in the persistent perianth. **Seed** albuminous. The flowers are anemophilous

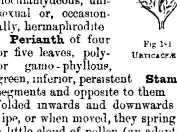


Fig 183 —FLORAL DIAGRAM OF URTICACEÆ. A Male, B, Female flowers.

The various kinds of "Artillery Plant" grown in our gardens are species of *Pilea* and are so called because of their explosive stamens

The chief plants of this order in India are the numerous herbs of the genera *Urtica*, *Pilea*, *Elatostema*, *Laportea* (Fever-nettle), *Girardinia* (Nilgiri Nettle), and others that grow in the hills. Species of *Boehmeria* and *Debregeasia*

yield a very tough and strong fibre from the bark, and *B. nivea* is sometimes cultivated for this (rhea, ramie, or China grass-cloth).

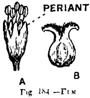


Fig. 184.—Elm.
A, Flower, B, Gynaeceum of flower

The order *Ulmaceæ*, of which *Ulmus* and *Celtis* are examples, is closely allied to the Urticaceæ, and represented in India by a few trees

Celtis.—The tree is evergreen, with polygamous flowers; P5, A4-5, G(2); fruit a drupe

§ 7 Moraceæ.

Distinguishing characters:—Trees and shrubs, with stipulate leaves and latex, and cymose inflorescence of unisexual flowers, P4 or (4), persistent, A4, opposite them, G(2), one carpel usually aborted except the style, ovary unilocular, with one ovule, fruit usually a multiple of achenes or drupes

This is a large order, well represented in India, composed of trees and shrubs with latex and with stipulate leaves, with cymose inflorescences, and unisexual flowers **Perianth** 4 or (4), **stamens** as many and opposite to them, **ovary** of two carpels, one of which, all but the style, is generally abortive, unilocular, with one usually pendulous ovule, which gives an achene or drupe Usually, however, the **fruit** is multiple, arising from the union of many different fruits, as already described for two of the members of this order, the *Ficus* and the Mulberry, on p 283. In *Artocarpus* the inflorescence becomes fleshy and has a texture resembling that of bread

Among the familiar plants belonging to this family in India are the many species of *Ficus*, including *F. bengalensis*, the Banyan, which produces aerial roots that come down to the ground and take hold there; in the famous example of this tree in the Calcutta Botanic Garden there are hundreds of these roots established, and the single tree covers several acres of ground. *F elastica*, the Rubber Tree of Assam, usually starts epiphytically, but soon gets its roots into the soil, and also forms enormous buttress roots at the base Other species start epiphytically, and form roots which clasp and ultimately strangle the host. *F religiosa* is the Pipul *F. elastica* produces caoutchouc or indiarubber, and several species

are used as hosts for the lac-insect. *F. Carica*, the Fig (Anjír); *F. glomerata* (Gúlar). *Morus alba*, var *indica*, is the Indian Mulberry, used for its fruit and to feed silk-worms. *Artocarpus integrifolia* is the Jak Fruit; *A. incisa* the Bread Fruit, introduced from the Pacific, and now common on the coasts. *Dorstenia indica*, with an open cup-like receptacle, occurs in Central and Southern India. *Cannabis sativa* is the Hemp, largely grown for its narcotic resin, which exudes from the plant, and occurs in three common forms, ganja, charras, and bhang; the first is the ♀ flowering tops consolidated, the second the resin only, the third the leaves. Hashish, an intoxicating liquor, is also prepared from it.

§ 8 Loranthaceæ.

Distinguishing characters.—Parasites with evergreen leaves and flowers in little groups of 3 or 2, ☿ or unisexual, epigynous. Stamens as many as, and united to, perianth leaves, ovary unilocular, the ovules not differentiated. Fruit a pseudo-berry or -drupe

This is a very interesting order of parasitic plants, in general well represented in India, chiefly by species of *Loranthus* They are semi-parasitic shrubs, which are attached to the host plants by suckers or haustoria, in the manner already described (p 197). The stem very commonly forms branches at each node, the main shoot dying off and leaving them, so that it is sympodially constructed As the suckers only draw material from the wood of the host, green leaves are an obvious necessity, and the plant possesses them, they may be opposite or alternate

The **inflorescence** is cymose, and the **flowers** occur in little groups of three, or sometimes of two only, the central one of the three aborting The **bract**, instead of coming off so as to subtend the flower, in cases where the latter has a stalk, is united to the stalk for some distance up, and looks like a bracteole. The **flowers** are either ☿ or unisexual, and possess a perianth of 3-5 leaves, either sepaloid or petaloid, with as many stamens inserted upon them The inferior ovary is unilocular, and the ovules are not differentiated until after pollination. The embryo-sacs are usually more than one in each ovule, and lengthened out. The **fruit** is a pseudo-berry or -drupe, the seed surrounded by a sticky layer of viscin, so that when a bird

swallows the fruit, it wipes off the seed upon a branch or elsewhere that it may be able to become parasitic. In Ceylon, the seeds may sometimes be found germinating upon telegraph wires

The order is divided into two suborders, one of which, the Loranthoideæ, possesses a calyculus, the other, the Viscoideæ, not. This is a little fringe below the perianth proper, about whose morphological nature there has been much discussion, some regarding it as a calyx. The many species of *Loranthus* belong to the first suborder, the few Viscums to the other.

Many species of *Loranthus* are common in India, and a few of *Viscum* and other genera may be sometimes seen These parasites are sometimes so common as to do great damage in gardens or on plantations.

§ 9 Polygonaceæ.

Distinguishing characters:—Flowers polypetalous, hypogynous, usually hermaphrodite; trimerous or sometimes dimerous, but the number of parts often increased by duplication or diminished by suppression Characters of ovary, ovule and fruit. The presence of an ochrea is characteristic of the order.

This order is represented in the Indian Flora in all parts by the genus *Polygonum*, while other genera, native or cultivated, are *Rumex* (Docks and Sorrels), *Rheum* (e g *R rhaponticum*, the Rhubarb, *R. officinale*, the medicinal Rhubarb), and *Fagopyrum*, the Buckwheat They are mostly herbs.

The leaves are simple and alternate, with ochreate stipules, and the stems are swollen at the nodes

The acid properties found in most of the plants are due to the presence of various oxalates (p. 41).

The **inflorescence** in most cases is mixed, commonly a raceme or panicle of cymes. The **flowers** are hypogynous and usually hermaphrodite

They are typically trimerous, sometimes dimerous, but the number of parts is often increased by duplication or diminished by suppression.

Unisexual flowers occur in the Sorrels; *Rumex acetosa*, the Sorrel, is monœcious; *R. acetosella*, the Sheep's Sorrel, is diœcious.

The **perianth** typically consists of three sepals and three petals resembling each other, and either sepaloid or

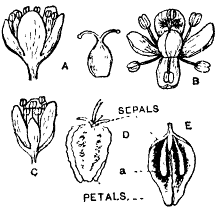


FIG 185 —POLYGONACEÆ.

A, Flower and pistil of *Polygonum Persicaria* (2 styles), B, Flower of *Oxyria*, C, Flower of a species of *Rumex*, D, E, Fruits of species of *Rumex* showing persistent perianth (a = swollen midrib of petal).

petaloid (Figs. 185 C, 186 A). It is polyphyllous, imbricate in aestivation, inferior and persistent. This typical condition is found in *Rumex* and *Rheum*, and in these genera the *inner* segments (petals) enlarge during the development of the fruit and invest it (Fig. 185, D, E) In *Polygonum* (Figs. 185 A, 186 B) the anterior segment of the inner series (petal) is suppressed, so that the perianth consists of five leaves (P3 + 2 or K3 C2), here the three *outer* segments become enlarged and invest the fruit. In *Oxyria* (Fig. 185, B) there are two sepals and two petals (P2 + 2 or K2 C2).

The **Andrœcium** consists typically of six stamens (A3 + 3), but this typical condition is seldom found

Usually there is chorisis of one or more of the stamens of the outer series, and this may be accompanied by suppression of one or more members of the inner series (see Fig 186) In *Rheum* there are nine **stamens**, all the outer stamens being duplicated (A3 × 2 + 3) In *Rumex* the outer are all duplicated, but the inner suppressed

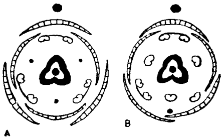


Fig 186 —FLORAL DIAGRAMS
A, *Rumex*, B, Species of *Polygonum*.

(A3 × 2 + 0) In *Polygonum* there are five to eight stamens, usually two outer stamens are duplicated, and one or more of the inner ones suppressed. In *Oxyria*, where the arrangement is dimerous, there are six stamens, the two outer ones being duplicated (A2 × 2 + 2).

The **Gynæceum** is usually tri-carpellary and syncarpous, in *Oxyria* and some species of *Polygonum* (e.g *P amphibium*) it is bicarpellary (Fig 185, A). The *ovary* is unilocular, superior, with one basal orthotropous ovule (Fig. 137, p 242), *stigmas* two or three. The **fruit** (Fig 185, D, E) is ovoid when there are two carpels, triangular when there are three. The persistent membranous perianth provides for wind dispersal The **seed** is albuminous

An annular honey disc is present in *Polygonum* at the base of the stamens, and the flowers are entomophilous Some species are marsh or water plants

In *Rumex* there is no honey disc The stigmas are long and

feathery, and the **flowers** are wind-pollinated. *Rumex crispus* is the Curled Dock; *R obtusifolius*, the Broad Dock; *R. Hydrolapathum*, the Water Dock *Rheum* is entomophilous. *Fagopyrum* resembles *Polygonum*, and is sometimes placed in that genus (*Polygonum Fagopyrum*)

§ 10. Chenopodiaceæ.

Distinguishing characters:—Flowers monochlamydeous, regular, hermaphrodite or unisexual, hypogynous, typically pentamerous Characters of ovary and seed. An order of halophytes.

The plants belonging to this order are widely distributed in maritime regions, many of them (halophytes) growing in salt marshes or on muddy foreshores, and showing marked xerophytic characters (see p. 217). It is represented in India by the Glasswort or Marsh Samphire (*Salicornia*), the Saltwort (*Salsola Kali*), the Seablite (*Suæda maritima*), and various species of Goosefoot (*Chenopodium*) and others *Chenopodium* is not so markedly halophytic as the other genera, various species being commonly met with on waste or cultivated ground and presenting the ordinary herbaceous characters

The plants are mostly herbs, in which the stem and leaves are often succulent and fleshy and serve for the storage of water. The leaves are occasionally absent (e g *Salicornia*), when present they are exstipulate and alternate, or occasionally opposite (sp of *Atriplex*) They often feel granular or mealy to the touch owing to the presence of small hairs; this is very noticeable in species of *Chenopodium* and *Atriplex*

The **inflorescence** is frequently mixed; racemes, panicles, and spikes of small cymes are common. The **flowers** (Fig 319) are small and inconspicuous, regular, monochlamydeous, hypogynous, hermaphrodite, or occasionally (*Atriplex*) unisexual and either monœcious or diœcious. They are honeyless, and either anemophilous or self-pollinated

Perianth poly- or gamo-phyllous, small, sepaloid, and persistent It usually consists of five leaves (the rule in *Chenopodium, Beta, Salsola,* and *Suæda*), sometimes of three or four (*Salicornia*); in the female **flowers** of

Atriplex there are only two **Stamens** usually as many as the leaves of the perianth and opposite them, hypogynous, sometimes perigynous (*Beta*); *Salicornia* has either one or two. **Gynæceum** of two, sometimes three, carpels, syncarpous; *ovary* unilocular, superior (half inferior in *Beta*) with one basal campylotropous ovule. **Fruit** a small nut enclosed in the persistent perianth. **Seed** albuminous or occasionally exalbuminous; the embryo is curved or spirally twisted round the endosperm.

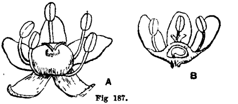


Fig 187.

A, Flower of species of *Chenopodium*, B, Flower of Beet in section

Salicornia, the Samphire, is a small leafless plant which is widely distributed and grows on muddy shores It has succulent jointed stems The flowers are placed two or three together in little cavities, two of which are found opposite to each other at each node The flower has a fleshy perianth with three or four teeth, one or two stamens, and a pistil of two carpels

There are some familiar cultivated forms The Garden Beet and the Sugar Beet are cultivated varieties of the Wild Beet They are biennials and sugar is stored up in their roots *Spinacia oleracea* is the Spinach, the flowers are in dichasia and are diœcious

§ 11 Portulacaceæ (Fig. 188).

Distinguishing characters:—Herbs, leaves often fleshy, flowers regular, ☿, *in cymes; sepals* 2, *petals* 4-5, *stamens* 4-5, *opposite the petals, or more, sometimes perigynous, ovary superior* (2-8), *usually* (3), *unilocular with few or many ovules on a central basal placenta, fruit a capsule.*

This order is well represented in India by the various species of *Portulaca* (Fig 188), which are common on waste ground and in sunny places. They are all small herbaceous plants growing only an inch or two high,

with many sprawling lateral branches. They are usually annuals, coming up afresh every year from the seeds of the previous year, but some have tuberous storage roots The **leaves** are small, and are generally more or less fleshy from the development of water-storing parenchy-

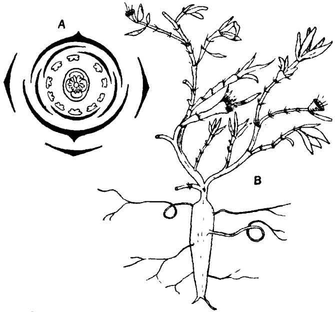


Fig 188 —A, FLORAL DIAGRAM OF *Portulaca oleracea* (AFTER ENGLER). B, PLANT OF *Portulaca tuberosa*

matous tissue; the plants grow in places which are liable to become very dry, and without storage of water as well as a cuticle which resists the passage of water by evaporation, they would be liable to destruction in a serious drought. The leaves are sometimes alternate, sometimes opposite, and usually possess stipules, though in some of the species these are represented by an axillary bundle of fine white hairs.

The **inflorescences** are simple, in many species the flowers are solitary, but in the others the inflorescence is of cymose nature

The **flowers** are hermaphrodite and regular and usually hypogynous, whether they are really dichlamydeous or not is a matter of discussion, but they are now perhaps most often regarded as only monochlamydeous. Assuming for the moment that they have the two whorls of perianth, the **calyx** is of two sepals, an anterior overlapping a posterior, and usually united below; the **petals** are 4 or 5, distinct, and in *Portulaca*, the only common genus of the family in India, they are markedly perigynous, the ovary being adherent to the base of the sepals The **stamens** are 4 or 5, opposite to the petals, or sometimes twice or three times as many, and sometimes, more especially in *Portulaca*, of intermediate numbers, due to more or less branching of one or more of their number, the **ovary** is usually superior, but in *Portulaca* is half-inferior, of (2-8) usually (3) carpels, and is unilocular with a basal placenta which bears numerous ovules, while the number of carpels is indicated by the number of stigmas.

The arguments upon which the theory of the monochlamydeous nature of this flower is based are chiefly that the petals and stamens are opposite to one another, instead of alternating, as they ought to do, and that the sepals are two instead of five, giving the impression that they are in reality the bracteoles of the flower, not the calyx This is to some extent confirmed by other phenomena to be seen in this and other allied families, and the evidence is on the whole in favour of this view, under which the apparent corolla is really the only whorl of the perianth.

The flowers secrete honey and are visited by flies and other insects They close at night and in dull weather On withering the stamens and style crumple up together, and self-fertilisation occurs The stamens of *Portulaca oleracea* are slightly sensitive to contact, and move towards the side touched.

The only Indian genus is *Portulaca* itself, though there are sometimes others to be seen in ornamental gardens The genus *Portulaca* is abnormal in possessing a semi-inferior ovary. Among the

common species are *P oleracea*, the Purslane, which is a common pot-herb in many parts of the world, and has alternate flattish exstipulate leaves, rather closely crowded together, and bunches of flowers; *P. quadrifida*, with opposite flat leaves, stipules composed of bunches of hairs, and single flowers, *P. tuberosa* (Fig 188, B), on rocks on the sea shore, with nearly cylindrical very fleshy leaves (p 433), and single flowers. There are many garden varieties of *Portulaca* cultivated.

§ 12 Caryophyllaceæ.

Distinguishing characters:—Flowers regular, generally polypetalous and hypogynous; stamens usually twice as many as the petals, but sometimes fewer; pistil of 2-5 *carpels, syncarpous, ovary unilocular; free central placentation, fruit a capsule; the swollen nodes, opposite leaves, and cymose inflorescence are characteristic*

The plants belonging to this order are mostly herbs with swollen nodes and opposite, simple, entire, and usually exstipulate leaves, *e.g* Pink, Sweet William, Chickweed, and various species of Campion The **inflorescence** is cymose, typically a dichasium (Fig. 152) The **flowers** are regular, usually hermaphrodite and pentamerous, exceptionally unisexual or tetramerous.

Calyx polysepalous or gamosepalous, of 5 (or 4) sepals **Corolla** polypetalous, of 5 (or 4) petals, occasionally the petals are wanting. **Andrœcium** of 10 (or 8) free stamens (in some species reduced to 5, 4, or 3), hypogynous (or, occasionally, perigynous), obdiplostemonous **Gynæceum** of 2-5 carpels, syncarpous, with free styles (Fig 132, C), *ovary* unilocular, superior; *ovules* usually numerous, amphitropous or campylotropous, with free central placentation (see p. 241). **Seed** albuminous, embryo curved round the endosperm. **Fruit** usually a unilocular capsule dehiscing by teeth separating at the apex, seeds scattered by the censer mechanism (p. 285).

In the Caryophyllaceæ there are two very distinct types of flower-structure, and corresponding to this the order is subdivided into two groups or tribes.—

I The **Alsinoideæ**, the lower type, in which the sepals are free or only slightly united at the base, and the petals

are short. The flowers are shallow and wide open therefore, and the honey, which is secreted by glands at the bases of the stamens, is accessible to a variety of short-tongued insects (flies, etc) The flowers are usually protandrous, but some are homogamous and self-pollinated. In this group the leaves are sometimes stipulate, the flowers may be more or less perigynous, and there is frequently reduction in the number of petals or stamens.

II. The **Silenoideæ**, in which the calyx is gamosepalous and tubular, and the petals are long and clawed (Fig 123, A). The flowers therefore are closed up, and the honey, which is secreted by the receptacle between the calyx and corolla, can be reached only by long-tongued insects (bees, butterflies, and moths). Small insects are further excluded in some species by the presence of ligules on the petals. The flowers are usually distinctly protandrous

I **Alsinoideæ** —*Stellaria*. Petals 5, deeply two-lobed, appearing like 10, rarely none. Many species are common in the hills, but a few descend to the plains, preferring moist, shady places *Cerastium vulgatum* is found in the hills all over India

II. **Silenoideæ.**—Species of *Dianthus*, *Lychnis*, and *Silene* are found in the hills. *S. conoidea* descends to the Punjab plains The genus *Silene* is distinguished from *Lychnis* by its three styles

§ 13. Ranunculaceæ.

Distinguishing characters:—Perianth leaves free, usually petaloid; flowers hypogynous; stamens indefinite (∞), *gynæceum apocarpous.*

Except *Clematis*, the plants belonging to this order are herbs with alternate or radical, and, usually, much-divided, exstipulate, sheathing leaves. Most species of *Clematis* are shrubs with *opposite* leaves, climbing by means of their petioles.

The plants usually perennate by means of sympodial rhizomes The primary root is lost and adventitious roots are developed In many cases these adventitious roots become tuberous, *e g.* in Monkshood.

The **inflorescence** is in most cases cymose, *e.g.* Buttercup. In Monkshood and Larkspur racemes are found. In *Anemone* the flowering shoot bears a terminal flower.

The **flowers** are hermaphrodite, mostly actinomorphic, and may be cyclic or hemicyclic. In Monkshood and Larkspur they are zygomorphic.

The **perianth** seldom shows distinct calyx and corolla. This does occur, however, in the largest genus *Ranunculus*, where there are typically five sepals and five petals (Fig 117). In many cases between the outer perianth leaves and the stamens there are honey-organs (nectaries) of various forms. These have commonly been regarded as *modified petals*. According to this view the outer perianth leaves represent a petaloid calyx. The term calyx is also applied to a single series of perianth leaves, when there are no honey-organs (e g. *Clematis*, *Thalictrum*), on the ground that in such a case the petals have disappeared altogether. It is convenient to adopt this view in describing the various types, although it is more probable that the honey-organs have been derived from the outer stamens It should be noticed that nectaries in some genera are developed in connection with the sepals, stamens, or carpels

The **stamens** are indefinite in number (∞), hypogynous, free; *anthers* innate, extrorse The **gynæceum** is apocarpous, and usually polycarpellary; the number of carpels varies. There may be one or a number of anatropous ovules in each ovary; if one, it may be erect or pendulous

The **seed** is albuminous. The **fruit** may be an etærio of achenes, or of follicles—rarely a berry, or (owing to exceptional fusion of the carpels as in *Nigella*) a capsule.

Pollination.—The flowers are usually protandrous, but those of *Thalictrum* and *Helleborus* are protogynous The Buttercup, in which the honey is only partially concealed, is visited by various insects. The flowers of *Adonis* and *Thalictrum*, as also those of Wood Anemone and Traveller's Joy, are "pollen-flowers"; but some species of *Thalictrum* are wind-pollinated, and in some species of *Anemone* and *Clematis* honey is secreted by staminodes only partially concealed.

The flowers of *Trollius* and Wood Anemone are often self-pollinated, and in most of the other genera self-pollination may occur, but in *Helleborus* it is precluded by the absolute protogyny of the flower The most highly specialised flowers are those of Columbine (*Aquilegia*), Larkspur, and Monkshood They are adapted for pollination by long-tongued bees (chiefly humble-bees).

Most of the Indian Ranunculaceæ grow in the hills, some ascending to the alpine zone in the Himalaya *Ranunculus scleratus* is, however, found in the plains from the Punjab to Bengal.

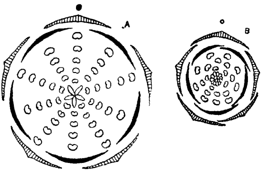


Fig 189 —FLORAL DIAGRAMS OF RANUNCULACEÆ. A, Aquilegia (Columbine), B, Species of Ranunculus

Ranunculus (Figs 117, 189B) This genus includes the Buttercups (Crowfoots) $K_5C_5A_\infty C_\infty$. Each petal has a little pocket-shaped nectary at the base Fruit an etærio of achenes

Clematis Four petaloid sepals, petals none; fruit an etærio of achenes with persistent hairy styles Many specimens common in Temperate Himalaya, e g *C montana*, *C Gouriana*

Anemone Sepals 5-9, petaloid, petals none, fruit an etærio of achenes *A rivularis*, etc, Himalaya

Thalictrum Sepals 4-5, more or less petaloid, falling off early, petals none The stamens form the attractive part of the flower Fruit an etærio of achenes *T javanicum*, *T foliolosum*, Himalaya.

Aquilegia (Fig 189A) Sepals 5, petaloid, petals 5, spurred; carpels 5, fruit an etærio of follicles *A pubiflora*, W Himalaya

Aconitum (Monkshood), Fig. 121: Zygomorphic; 5 petaloid sepals, the posterior one large and galeate; 2 petals represented by nectariferous organs enclosed in the hood of the calyx, carpels 2-5, fruit an etærio of follicles. *A. heterophyllum* is the Atís, the roots of which are largely collected in the W. Himalaya and exported to the plains for medicinal purposes.

Delphinium (Larkspur) · Zygomorphic; 5 petaloid sepals, the posterior one spurred, 2 spurred petals projecting into the spurred sepals; carpels 1-5, fruit an etærio of follicles, sometimes a single follicle

§ 14 Anonaceæ.

Distinguishing characters:—Trees and shrubs with two-ranked entire exstipulate leaves and ☿ hypogynous flowers; perianth usually in three whorls, stamens and carpels ∞, free; ovules ∞; fruit usually an aggregate of berries

This is a large order of tropical trees and shrubs, well represented in the East by the custard apples (Sharífa or Sítáphal) and soursops (Mamphal), etc Their leaves are usually borne in two ranks upon the lateral branches, and have no stipules, they are also undivided

The **inflorescence** may be of various kinds, and the flowers are ☿ and regular. The **perianth** consists of three or more whorls of usually three leaves each, the outer whorls being sepaloid, the inner petaloid, the **stamens** are ∞, in a spiral arrangement, and like the perianth hypogynous, while the **carpels** are also ∞ and free from one another, except in *Monodora*, which is rarely seen in India. The ovules in each carpel may be one or many, anatropous. The **fruit** is most commonly an aggregate of berries, which are sometimes constricted between the seeds. In the custard apples, soursops, and others of the genus *Anona*, the berries are united to the receptacle, forming a single fruit from an apocarpous ovary. The Magnoliaceæ, which are represented in India by the Champak (*Michelia Champaca*) and others, have almost the same general characters, and the chief point of distinction lies in the fact that the endosperm of the seeds in Anonaceæ is ruminate, or marked by wavy lines which give it a kind of marbled appearance

There are many Anonaceæ in India, but the only familiar

ones are the various species of *Anona*, *A. muricata*, the Soursop (Mamphal), *A. reticulata*, the Bullock's Heart (Rámphal), and *A. squamosa*, the Custard Apple (Sharífa or Sítáphal).

§ 15 Lauraceæ.

Distinguishing characters:—Trees and shrubs with alternate exstipulate leaves and regular apetalous flowers, most often trimerous with two whorls of perigynous perianth, three or four of stamens (anthers opening by valves) and unilocular ovary. Fruit a berry.

This is a fairly large order of tropical trees and shrubs, especially well represented in Indo-Malaya. They have a somewhat xerophytic character, which is shown in the leathery leaves that most of them possess, and which are alternate and exstipulate, and usually possess many oil-cavities, which show as translucent dots when held up to the light. *Cassytha* is an interesting parasite with the general habit and construction of *Cuscuta*, already described (p. 196).

The **inflorescence** is of various kinds, either racemose or cymose, and is composed of regular flowers, which may be either ☿ or unisexual. The parts of the **flower** may be of almost any moderate number in any whorl, but the numbers in general correspond from one whorl to another, and the most common number is three. The **perianth** is in two whorls, sepaloid and perigynous, the **stamens** in four whorls, sometimes epigynous, the carpel one forming a unilocular **ovary** with one pendulous anatropous ovule. The anthers are most commonly all introrse, but sometimes those of the third whorl open outwards; the opening is by valves which bend upwards. The **fruit** is a berry, and is often enclosed in the receptacle which also becomes fleshy; the **seed** is exalbuminous.

There are many of this order in India, but among the more important are *Cinnamomum zeylanicum*, the Cinnamon (Dálchíní), a tree if left to itself, but in cultivation kept coppiced to produce long shoots, whose bark, stripped off, dried, and rolled up, forms the spice of commerce; *C. Camphora*, the Camphor (Káfúr), a native of

China and Japan, but sometimes cultivated, the leaves being distilled for the camphor which they contain, the Alligator Pear or Avocado, *Persea gratissima*, an American fruit introduced by the Portuguese and now very common, with one gigantic seed in the middle of a fleshy fruit; *Cassytha*, the parasite mentioned, etc, etc.

§ 16. **Cruciferæ** (Figs. 128, 164).

Distinguishing characters :—Flowers polypetalous, hypogynous ; parts in twos or fours ; cruciform corolla, tetradynamous stamens ; placentation and structure of ovary and fruit.

This is an almost cosmopolitan order, but much better represented in temperate than in tropical climates, though the Mustard, which belongs to this family, is everywhere to be found in India It is almost entirely composed of small herbs, and is a very distinct and well characterised family, with alternate exstipulate leaves

The **inflorescence** is usually a typical raceme or corymb, and only very rarely has it any trace of bracts or of bracteoles. The **flower** is ☿, regular, and hypogynously arranged The **calyx** is composed of four distinct sepals, the **corolla** similarly of four petals, which are arranged like the arms of a Greek cross, whence the name of the order The **stamens,** whose anthers are introrse, are arranged in two whorls, outside are two shorter stamens, inside are four longer ones; this arrangement, which is characteristic of the family, is termed *tetradynamous* The **carpels** are two, arranged transversely in the flower, they are united, and form an *ovary* which is "typically" unilocular, but in practice bilocular, for the two parietal placentæ are united by a thin membrane crossing the ovary in the anteroposterior direction (Figs. 128, 141). The ovary terminates in a very short style, bearing two stigmas, which stand, not above the midribs, but above the placentæ. The **fruit** is capsular, and may be long and comparatively narrow, in which case it is called a *siliqua*, while if shorter and broader it is termed a *silicula*, when it opens, the two valves break away from the replum, except at the upper end (p. 277, Fig 164), leaving the replum intact, usually with most of the seeds adhering to it.

Honey is secreted by **nectaries** which may be seen on the basal portions of the stamens, and is more or less protected in most Cruciferæ by the fact that the sepals often stand up nearly vertically, forming a sort of tube to the flower Insect visitors touch the stamens with one side of their heads and bodies, the stigmas with the other

There are not many wild Cruciferæ in India, but several important cultivated species, e g *Brassica alba*, the Mustard, *B campestris*, the Turnip, *B oleracea*, the Cabbage, with the varieties Cauliflower, Knol-kohl (with the base of the stem thickened), etc ; *Nasturtium officinale*, the Watercress, *Raphanus sativus*, the Radish *Capsella Bursa-Pastoris*, the Shepherd's Purse, is a common weed.

§ 17 Rosaceæ.

Distinguishing characters:—Flowers polypetalous, perigynous, regular; stamens in whorls, usually numerous; pistil apocarpous.

This is a large order of herbs, shrubs, and trees The leaves are alternate, simple, or compound, and usually stipulate Vegetative reproduction by means of runners and suckers is of common occurrence. The order is distinguished from Ranunculaceæ by the shape of the receptacle, and the whorled arrangement of the floral leaves Familiar examples are Rose, Strawberry, Raspberry, Apple, Pear, and Quince

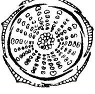


Fig 190 --FLORAL DIAGRAM OF ROSE

The **inflorescence** is very various, and includes both racemose and cymose forms. The **flowers** (Fig 190) are regular, pentamerous (or tetramerous), usually hermaphrodite, perigynous (occasionally epigynous, owing to fusion of the carpels with the calyx tube)

The **calyx** is gamosepalous, of five (or, occasionally, four) sepals An epicalyx is *sometimes* present, *e g* Strawberry. The **corolla** is polypetalous and rosaceous, with usually five petals, imbricate in the bud, the petals are occasionally wanting **Stamens** two, three, or four times

as many as the petals, or ∞. **Gynæceum** of 1 to ∞ carpels, apocarpous. There are usually 1 to 2 anatropous ovules in each carpel. **Fruit** various—a drupe, a pome, etærios of drupes, achenes, or follicles. The **seed** is exalbuminous

The order gives a good illustration of the various forms of perigyny (see Fig 119, B–E). The great variety of fruits is due to various causes—persistence or non-persistence of the receptacle (calyx-tube), dryness or fleshiness of pericarp or receptacle, number and form of ripe carpels, etc.

The wild members of this order are mostly found in the hills

Prunus Fruit a drupe *P. armeniaca* (Zardálú), Apricot, *P. persica* (Arú), Peach; *P Amygdalus* (Bádám), Almond, *P. communis* (Alúchá), *P lanata* (Amlok)

Spiræa Fruit an etærio of follicles more or less united at the base, inflorescence a raceme, corymb or panicle. *S. canescens*, *S belli*, Temperate Himalaya

Rubus Fruit an etærio of succulent drupes, receptacle flat; calyx persistent; no epicalyx Many species with edible fruits (Raspberry, Blackberry)

Potentilla Fruit an etærio of achenes on a dry receptacle, calyx persistent, epicalyx present Some species ascend into alpine Himalaya

Fragaria (Strawberry) Fruit an etærio of *dry* achenes embedded in a *fleshy swollen receptacle* (ct *Rubus*) *F indica* and *F vesca* (Wild Strawberry) Himalaya

Rosa (Rose) Fruit of many achenes enclosed in a deep, hollow fleshy receptacle

Pyrus Fruit a pome, the carpels being adherent to the fleshy receptacle, 2 seeds in each carpel *P communis* (Náspátí), Pear, *P Malus* (Seb), Apple

Cydonia Fruit a pome, a number of seeds in each carpel. *C. vulgaris* (Bihi), Quince

§ 18. Leguminosæ.

Distinguishing characters.—Trees, shrubs, and herbs, often climbing; leaves alternate, stipulate, usually compound; flowers regular, or more often irregular, in racemose inflorescences, slightly perigynous; sepals usually 5, united, petals 5, free, often highly zygomorphic, with standard, wings, and keel, stamens 10, free or united into a

tube, sometimes ∞ , *carpel* 1, *superior, with long style; fruit a legume or pod, or lomentum, with exalbuminous seeds.*

This is one of the largest orders in the Indian flora, and is divided into three sub-orders, Papilionatæ, Cæsalpinioideæ and Mimosoideæ (p 324), each of which is well represented in India Living in every variety of soil and climate, they show great variety in habit—trees, shrubs, herbs, water-plants, mesophytes, xerophytes, climbers, etc

The roots of most species exhibit peculiar tubercles, which may be seen by taking up a root with the soil attached, and carefully washing away the latter in water These **tubercles** are metamorphosed lateral roots, and are inhabited by a **bacillus** which enables the plant to absorb free nitrogen from the air. Hence the great value of the Leguminosæ as a crop on poor soil, as coming in a rotation of crops, or as forming part of a mixture of crops such as is often employed in India (pulses or Leguminosæ being sown intermixed with cereals such as *Sorghum*) They are also of much value when employed as manures for tobacco or other crops In all these cases the soil is enriched to a greater or less extent with nitrogen, which is one of the most expensive constituents in an artificial manure. It is almost needless to remark that if the leguminous plant be made to yield a crop, so much nitrogen will be removed in this that the gain to the soil will be little or nothing, whereas if the whole plant be employed as green manure, the gain will be considerable.

The **stem** is most commonly erect, but there are also many climbing plants Some of these, for example the peas, have tendrils which are modified leaves, some of the Bauhinias and others have stems modified to serve as tendrils, some of the Cæsalpinias have leaves modified into hooks, some Acacias have hooks which are simple emergences A good many of the family have thorns, which in some cases, as in many Acacias, are modified stipules.

The **leaves** are generally alternate, stipulate, compound, pinnate. Some of the Acacias cultivated in the hills, especially *A. decurrens*, exhibit phyllodes, and if seedlings be studied, they will be seen to exhibit an

interesting gradual transition, the first leaves produced are ordinary pinnate leaves, the next have rather less of the pinnate portion and a somewhat flattened stalk, and so on it goes, till after a time the plant produces only leaves with flattened stalks and no pinnate blades at all The **stipules** in this family may assume a variety of forms; sometimes they are very large and leafy, as in some of the peas, but most often perhaps they take the form of thorns

At night, and in dull weather, the leaves very commonly perform **sleep movements** · these are effected by the leaflets folding together in pairs, either above or below

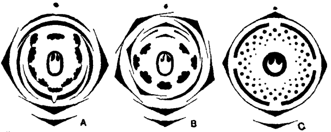


Fig 191 —FLORAL DIAGRAMS OF (A) *Vicia Faba* (PAPILIONATÆ) AFTER EICHLER, (B) *Cassia floribunda* (CÆSALPINIOIDEÆ) AFTER BAILLON, (C) *Acacia latifolia* (MIMOSOIDEÆ) AFTER EICHLER

the rachis, so that the amount of radiation from the leaf is very much reduced.

In *Mimosa pudica*, the Sensitive Plant, a Brazilian species now a common weed in some parts of India, the leaves are also sensitive to touch. A leaf should be very carefully touched at the outer end of one of the four segments; if the right degree of stimulation be given, the leaflets will be seen to close up in pairs, the stimulus working gradually downwards to the junction of the four segments, which will then be seen to move inwards towards one another, and after some time the main stalk will often bend downwards at its junction with the stem If the under side of this main joint be tickled in another leaf, it will move without causing any movement of the

other pulvini. *Neptunia oleracea*, a native water plant, shows similar phenomena, though not so well In *Desmodium gyrans*, the Telegraph Plant, which occurs all over India, the two lateral leaflets execute continual spontaneous rotary movements, so long as the temperature is high enough.

The **inflorescence** is racemose, but varies much in detail, panicles, spikes, and racemes all being common The **flowers** (Figs 191, 192) are regular in Mimoseæ,

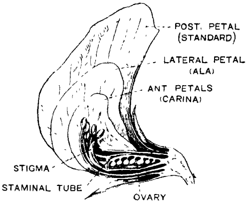


Fig 192 —Vertical Section of Flower of Pea.

irregular in the other sub-orders. The receptacle is convex or flat, so that at most the flower is only slightly perigynous. The **calyx** is usually (5), with the odd sepal anterior, the sepals more or less united, the **corolla** 5, alternating with the calyx, in æstivation it may be valvate (Mimoseæ) or imbricate, in the latter case the imbrication is ascending in Cæsalpinioideæ, the edges of the posterior petal being inside those of the lateral petals, and descending in Papilionatæ, the edges of the posterior petal being outside those of the lateral

The flower in Papilionatæ (Fig 192), and to a less extent in Cæsalpinioideæ, is irregular, having a large

posterior petal, the standard or *vexillum*, two laterals, the wings or *alæ*, and two lower, which are often united to form a keel or *carina*.

The **andrœcium** consists typically of 10 stamens, free or united into a tube, which may consist of all 10, or more often of 9 with a single free stamen lying along its upper side. Numerous stamens occur in some of the Mimoseæ, as in *Acacia*, *Albizzia*. When a keel is present, the stamens are enclosed in it. The **gynæceum** consists of one carpel, with the ventral side posterior, with a long style and terminal stigma, and has two rows of ovules alternating with one another to stand in one rank.

As regards **fertilisation** of the flower little is known except in regard to Papilionatæ. In these the keel encloses the stamens and style, and protects them from rain, the attacks of injurious insects, etc., while at the same time making the flower complex, so that the less intelligent insects do not visit it. Honey is secreted near the base of the tube of stamens, on the inner side, and is rendered accessible by the loose stamen on the upper side of the tube, which often also has two little openings on either side.

The flowers are thus especially adapted to bees, which are the cleverest insect visitors, but other insects at times visit them. The visitor alights on the wings and depresses them while looking for honey, and as the wings are always joined to the keel by projections which just fit into hollows in the latter, the keel is depressed also and the essential organs of the flower emerge. As the stamens come out later than the style, there is therefore a fair chance of cross-pollination happening, whilst self-pollination usually occurs also when the organs return into the keel on the departure of the insect. There are many different types of this mechanism, sometimes the parts simply move in and out as the keel is depressed or raised, sometimes they explode outwards at the first depression, and will not return, sometimes there is a mechanism, such as a brush of hairs on the style, for pushing out the pollen at the apex of the keel. In *Arachis*, the Ground-nut (Mung-phali), the flower after fertilisation buries itself in the earth and there ripens its pods.

The **fruit** is typically a legume or pod, formed of the one carpel, opening on *both* sides, very often, however, the pod is constricted between the seeds, forming a *lomentum*, which breaks up into one-seeded indehiscent portions as in *Desmodium* *A arabica* has also a pod much constricted between the seeds, but the whole pod dehisces imperfectly into two valves The **seed** is exalbuminous, and has generally thick cotyledons that contain much reserve material, ensuring rapid and vigorous germination.

Apart from their usefulness as green manures, the Leguminosæ are a most valuable order of plants. The seeds of many are important foods, though some are poisonous, and it is not safe to assume that a given member of the order can be used for food *Arachis hypogæa*, the Ground-nut, *Cicer arietinum*, the Chaná, *Dolichos Lablab*, the Lablab, *D. biflorus*, the Horse-gram, *Lens esculentus*, the Lentil, *Phaseolus Mungo*, the Mung, and other species of *Phaseolus* and *Pisum* (peas), and other members of the family, are important food crops in India Many have edible pods, *e g* the Tamarind, *Tamarindus indica*; others are valuable as fodder for animals. Many yield useful timbers, which in many cases, *e g.* the Tamarind, has the heart-wood darker-coloured than the sap-wood.

Crotalaria juncea is the Sunn-hemp, and other species also yield useful fibres. Several species of *Indigofera* yield indigo; the plant is soaked in water, and the yellowish solution thus obtained is oxidised by admission of air, when an insoluble precipitate of indigo is formed Oil is obtained from the seed of the Ground-nut and others, kino (a resin-like body, soluble in water, astringent, used in medicine and in tanning) from *Pterocarpus* and *Butea*, gums from *Acacia*, cutch, the yellowish tan used in the manufacture of khaki, from *Acacia Catechu*, and so on.

I. *Mimosoideæ* Aestivation of corolla valvate, flower regular.

II *Cæsalpinioideæ*. Aestivation of corolla imbricate, the posterior petal included by the laterals, flower zygomorphic, stamens usually free.

III. *Papilionatæ*. Aestivation of corolla imbricate, the posterior petal including the laterals; flower zygomorphic, stamens usually united, and enclosed in the keel

The number of Leguminosæ in India is enormous, and we may just mention a few in addition to those which have already been introduced. To **Mimosoideæ** belong *Mimosa pudica*, the Sensitive Plant, a Brazilian species introduced in early times by the Portuguese, probably accidentally, and now one of the commonest and most troublesome weeds in some districts, *Pithecolobium Saman*, the Rain-tree, also an introduction, now very largely used in some parts as a roadside shade tree, and showing nocturnal sleep movements very perfectly; *Acacia arabica*, the Babul, which in many parts of India is almost the only tree, many other species of *Acacia*, including the phyllode-bearing Australian *A. decurrens*, now much cultivated in the hills, *Neptunia oleracea*, a water plant with sensitive leaves; *Albizzia Lebbek*, the Siris. The Kathá, commonly eaten with Pán, is the heart-wood of *Acacia Catechu*, boiled down

To the **Cæsalpinioideæ** belong the Bauhinias, with watch-spring tendrils and two-lobed leaves (hence the name given to them, the two Bauhins, after whom they are called, being twins), the many Cassias, which with their bright yellow flowers form such a conspicuous feature in the vegetation of any weedy spot; *Cassia Fistula*, the Amaltás; *Cæsalpinia pulcherrima*, the Peacock Flower, everywhere cultivated, *Poinciana regia*, the Gold Mohur Tree; *Tamarindus indica*, the Tamarind, everywhere cultivated for its fruit, *Hæmatoxylon campechianum*, the heart-wood of which yields the dye hæmatoxylin, and others

To the **Papilionatæ** belong many species of *Crotalaria*, including *C juncea*, the Sunn Hemp; *Sesbania grandiflora*, the flowers of which are eaten, *Arachis hypogæa*, the Ground-nut; many Desmodiums, *Abrus precatorius*, the Crab's-eye, Rati, with its seeds sharply marked into red and black areas*, *Aeschynomene aspera*, the Shola, which grows as a low tree in shallow water and has the lower part of the stem, in or near the water, much thickened by a great development of spongy wood, which probably has to do with the æration of the plant†; *Pterocarpus*, of which several species

* These are the original of the carat weight of jewellers, and are used as weights in India

† This spongy wood is employed, cut into thin strips and fastened together, to make the pith helmets or topees worn by Europeans in India, which are often in error called solar, instead of shola, topees.

yield good timber, *Dalbergia latifolia*, the Blackwood or East Indian Rosewood, *D. Sissoo*, the Shísham, *Butea frondosa*, the Dhák or Pulás, one of the most showy flowering trees, from whose bark Bengal kino (see above) is obtained *, and the many species of *Phaseolus*, *Lathyrus*, *Vigna*, and other plants with edible seeds or pods, which are cultivated as garden and sometimes as field crops *Trigonella Fœnum-Græcum*, the Fenugreek, is the Methí. *Alhagi maurorum* is a desert plant occurring in Egypt, and in the plains of the Punjab and United Provinces, and bearing flowers on branches modified into thorns

§ 19. Rutaceæ.

Distinguishing characters:—Shrubs and trees with gland-dotted leaves, and ☿ flowers with large disc below ovary, calyx and corolla 5-4, stamens 10, 8, or less, ovary superior, of usually (5-4) carpels, multilocular, fruit various.

This is a large order, more characteristic of the subtropical than of the tropical zones, but well represented in India by oranges, limes, etc They are nearly all trees or shrubs, with alternate or opposite leaves, which are generally compound without stipules The leaves have oil-glands embedded in them, which show as translucent dots when held up to the light In *Citrus*, the genus to which belong oranges, limes, etc, the leaf is apparently simple, but the winged petiole is articulated to the lamina, which indicates that it is really one leaflet of a compound leaf (Fig. 99).

The construction of the **inflorescence** is generally cymose, and the **flowers** are most often ☿ and regular, with a large disc below the ovary. The **calyx** and **corolla** are 4 or 5 each, and the sepals and petals are free from one another; the **stamens** twice as many or sometimes as many, or ∞, with introrse anthers, the pistil of 4 or 5 carpels syncarpous, *ovary* superior, with as many loculi and axile placentation, and with two or more ovules in each loculus The **fruit** is of various kinds, a schizocarp,

* This plant is also used as a host for the lac insect, which feeds upon the tree and secretes around itself a resinous coating, which when collected and melted forms the shellac of commerce. The petals yield a yellow dye commonly used in the Holí festival.

berry, or drupe That of the Orange and Lime, for example, is a berry with a leathery epicarp, the flesh made up of cells which grow out from the inner layer of the pericarp.

The most familiar members of this family in India are the various species and varieties of *Citrus*, such as C *Aurantium*, the Orange, *C. Medica*, the Citron, with its varieties, *Limonum*, the Lemon, *acida*, the Lime, and *Limetta*, the Sweet Lime, *C. decumana*, the Shaddock or Pomelo (Chakotrá), etc., *Aegle Marmelos* is the Bael Fruit, *Feronia elephantum*, the Elephant Apple, *Murraya Koenigii*, the Curry Leaf (Gándhelá), etc., and there are many wild members of the family, chiefly belonging to the same sub-order, Aurantioideæ, as the oranges, etc. The twigs of *Zanthoxylum alatum* (Tirmar or Tejbal) are used as tooth-brushes The dried leaves of *Bœnninghausenia albiflora* (Pissu Már, Flea-killer) are believed to be effective against fleas

§ 20. Euphorbiaceæ.

Distinguishing characters.—Shrubs, trees, and a few herbs usually containing latex, leaves usually alternate and stipulate, inflorescence complex, often racemose at first and cymose later, of regular, hypogynous, unisexual flowers, perianth of two or, more often, one whorl, or none, usually 5-merous, stamens 1—∝, free or united in various ways; ovary usually (3), trilocular with axile placentas and often bifid styles, and 1 or 2 ovules in each loculus. fruit usually a schizocarp-capsule with albuminous seed.

This is one of the largest orders of the Flowering Plants, and is very well represented in India by many common weeds, many trees, and the large cactus-like fleshy Euphorbias (*E. Royleana*) of dry places. Though the **flowers** often have no corolla, and thus at first sight look very primitive, it would appear probable that they are in reality derived from ancestral forms which had rather better developed perianths, and they are closely related to the Geraniaceæ, the Rutaceæ and many orders of that group, which are by no means primitive.

The order shows considerable variety in habit, but in general they are mesophytic plants with a tendency towards xerophytism, which is often shown in leathery leaves with thick cuticle The highly xerophytic cactus-like fleshy Euphorbias, which are so common in dry rocky places in some parts of India, are specially interesting in this connection Their thick fleshy **stems,** covered with thick cuticle, prevent evaporation of water, which is also retarded by the thick nature of the sap. Only a small surface, in comparison with the bulk of the plant, is exposed to evaporation The **leaves** are small and fleshy, and soon after they have emerged from the bud they fall off, and are represented simply by a pair of thorns, the stipules of the former leaf, the chief feature of distinction between these plants and the cacti which they so closely resemble when not in flower The thorns in the latter are in little irregular groups, and represent the leaves of the axillary shoot arising at the point where they stand.

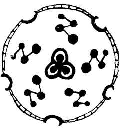


FIG 193.—DIAGRAM OF CYATHIUM OF *Euphorbia*.

The leaves are in general alternate, but sometimes opposite, and in some cases both forms of arrangement may be found on the same plant. **Stipules** are usually present, and in the fleshy Euphorbias and other forms are represented by stout thorns Nearly all the plants of the family, except the species of *Phyllanthus* and their allies, which are common in India, contain **latex** in special laticiferous cells In the indiarubber trees of the family, which are by far the most important sources of indiarubber, though at a former time the Indian *Ficus elastica* (Moraceæ) was a great source, this latex when dried forms the rubber of commerce These rubber-yielding Euphorbiaceæ are not natives of India, though largely cultivated there, but come from South America, and include *Hevea brasiliensis*, the Pará rubber, *Manihot Glaziovii*, the Ceará rubber, and others The latex runs out from incisions made in the

stem, and is nowadays usually made to coagulate by the addition of acid and in other ways, instead of being simply allowed to dry.

The **inflorescence** is often rather complex, and is usually cymose, though the first branching is frequently racemose. In *Euphorbia* itself it is condensed in such a way as to give the appearance of a single flower to what is in reality a group of male flowers surrounding a female (cyathium, p. 255, and Figs. 156, 193). The flowers themselves are always unisexual, but may be mono- or di-œcious

The **flower** (Fig 194) is regular and hypogynous, and a perianth may or may not occur; if present it is usually only of one whorl, but two are sometimes found. It is usually 5-merous The **stamens** are 1—∞ , free, or united in different ways, in the Castor-oil, for example, there are much branched stamens. The **ovary** is generally (3), 3-locular with axile placenta, with 3 styles which are most commonly again branched each into two The **ovules** are the same throughout the family, and form one of its best distinguishing marks, being 1 or 2 in each loculus, side by side, anatropous, pendulous, with the raphe towards the axis, and the micropyle usually covered by a caruncle, which is often found also on the seed. The **fruit** (a schizocarp-capsule) splits into carpels which at the same time open ventrally, the seeds are albuminous.

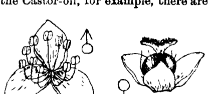


Fig 194 —MALE AND FEMALE FLOWERS OF *Euphorbiaceæ*

Many of the family are of economic importance, especially the rubber-yielding Manihots and Heveas, already mentioned, the Castor-oil, *Ricinus communis*, the Croton-oil, *Croton Tiglium*, and others

Among the more important native or cultivated genera in India are *Phyllanthus*, many species of which are common weeds, and which possess no latex, the fruit of *Phyllanthus Emblica* is the Amlá, which is commonly pickled, and also used in medicine;

Ricinus communis, the Castor-oil (everywhere wild or semi-cultivated, though originally a native of Africa), with much branched stamens and an explosive fruit, whose seeds contain an oil which is much used as a lubricant and in medicine, *Hevea brasiliensis*, the Para (Amazon) Indiarubber, introduced from South America to Ceylon and Singapore in 1876*, *Manihot Glaziovii*, the Ceara rubber of Brazil, which is a tree that sooner comes to a producing stage, but does not yield so much rubber as *Hevea*, and is but little cultivated, *Manihot utilissima*, the Bitter, and *M. Aipi*, the Sweet, Cassava or Manioca, both of which have large tuberous roots containing much starch †, *Codiæum variegatum*, the Croton of gardens, familiar everywhere for its variegated leaves, often of very peculiar shapes, with portions of naked petiole separating the different parts of the leaf, *Euphorbia* itself, of which there are many species in India, including many small herbaceous plants, but also including the great cactus-like species, e g *E Royleana* and others, which are so often to be seen on rocks and in other dry places, and which have thick fleshy angled stems *E tirucalli*, the Milk Hedge, is another very familiar species, introduced from tropical Africa, but now

* This tree was cultivated in the Botanical Gardens in Ceylon and Singapore for many years, taken up by planters from 1896 onwards, and is now cultivated on an area of at least a million acres in southern Asia and in other parts of the tropics. The rubber is obtained by tapping the bark, at first this was roughly done with a mallet and chisel, but now it is done with a knife, the cutting is usually done by making a vertical cut to a height of 5 or 6 feet and lateral sloping cuts leading out of it, and the further tapping is done by shaving a very thin portion off the lower side of these lateral cuts A remarkable phenomenon is exhibited in this species, although not in the other members of this family that have been tapped for rubber when a tree is first tapped it yields a small flow of latex, while at the second tapping, if performed within ten days, a much larger amount flows, and this may increase again at succeeding tappings, until a steady flow is reached, which will then continue almost unaltered for a long period, this reaction is termed the wound-response The milk collected is coagulated usually by means of acetic acid, pressed, and dried The amount of rubber obtained from this tree is very considerable, an average tree seven years old yielding about two to two-and-a-half or more pounds a year, while from one of the original Amazon trees grown at Henaratgoda in Ceylon, and now 36 years old, no less than 240 lb of dry rubber has been taken in three years.

† These form valuable foods, the former, however, contains prussic acid when fresh, and in consequence is dangerous to eat until the acid has been driven off by boiling or roasting, the starch in these roots is made into tapioca in some countries, by being carefully washed, and then gently heated while still in a wet condition

everywhere common, with its cylindrical stems adapting it to resist drought. *Croton Tiglium* is sometimes cultivated for the oil which its seeds contain, and which is a purgative of extraordinary efficacy *Buxus sempervirens*, the Box, occurs in North-Western India.

§ 21. Anacardiaceæ.

Distinguishing characters.—Trees and shrubs with alternate exstipulate leaves and flowers in panicles, usually 5-merous, but with stamens less than 10, and carpels usually 3, free, superior, fruit various

This is an important order, mainly tropical, composed of trees and shrubs with alternate exstipulate leaves, which are not gland-dotted, so that, though very close to it in many ways, the order cannot be confused with Rutaceæ

The **flowers** are arranged in panicles, and are usually ☿ The **sepals** and **petals** are 5 each, separate, the **stamens** typically 10, but usually with one or more missing, the **carpels** are commonly three, very seldom united. Quite often only one of the three carpels is fertile, and sometimes only one occurs at all. The *ovule* is single, anatropous

The **fruit** is various, that of the Mango being a drupe, that of the Cashew-nut a nut perched upon a swollen fleshy receptacle, and other types occur

Among the chief members of this family occurring in India are the Mango, *Mangifera indica*, the Cashew-nut (Káju), *Anacardium occidentale*, an American species introduced at an early date, *Spondias dulcis* and other species of Hog-plum, and many species of *Semecarpus*, some of which yield a useful black resin The seed of *S anacardium* is the Bhiláwá, the juice of which is used in marking cotton clothes *Pistacia vera* yields Pistachio Nuts (Pista)

§ 22 Sapindaceæ.

Distinguishing characters;—Trees, shrubs, or climbers, with alternate usually compound leaves, and cymes of flowers; calyx and corolla usually 5; stamens usually 10 with disc below; carpels 3, ovary trilocular, superior; fruit various.

Most of this large tropical family consists of trees and shrubs, but *Cardiospermum*, which is very common, is

herbaceous, and there are a few climbers, which mostly have the peculiar hooks elsewhere (p. 83) mentioned, composed of modified inflorescence axes, which thicken after clasping. The **leaves** are alternate, and have stipules in the case of the climbing species, they are generally compound pinnate, and sometimes have a terminal leaflet, sometimes have the end leaflet of an equally pinnate leaf bent round to serve as a terminal leaflet

The **inflorescence** is cymose, and the flowers, though they generally look as if hermaphrodite, are really unisexual, for the anthers are often well developed in the female flower, though containing no good pollen. The **flowers** are regular or zygomorphic; the **sepals** and **petals** are 5 or 4, the former sometimes, but rarely, united. The **stamens** are usually twice as many, but often two are absent, and sometimes they are only 5 or 4, or may even be ∞ The **ovary** is superior, usually of three carpels, trilocular, with a terminal style, and one ovule in each loculus The **fruit** is perhaps most often dry—a capsule or nut—but berries and drupes are not uncommon Often the nut has wings and becomes a samara

Several Sapindaceae of Indo-Malaya give useful fruit, especially *Nephelium lappaceum*, the Rambutan, and *N Longana*, the Longan The Litchi of China, *Litchi chinensis* (Lichi), is often cultivated in India The edible part of the fruit in these three species is the fleshy arillus, which is enormously enlarged and completely surrounds the seed. Many Sapindaceæ yield valuable timber The fruit of *Sapindus Mukorossi* and *S laurifolius* is the Rítthá or Soap-nut, the pericarp of which is widely used in India as a useful substitute for soap, especially for washing woollen and silken clothes *Dodonaea viscosa* (Sanatta, Kharata) grows wild over large areas of dry uncultivated land in North-West and Central India, as well as in the Deccan, and is also frequently planted in hedges The leaves are covered with a viscid resinous secretion, and the fruit is three-winged

§ 23 Balsaminaceæ.

Distinguishing characters:—Herbs with alternate leaves and ☿ zygomorphic flowers; calyx 5, the posterior one spurred, the two anterior small or absent; corolla 5, the

laterals united in pairs; stamens 5, with coherent anthers; ovary superior, 5-locular, with ∞ ovules; fruit an explosive capsule

This order practically consists of the one large genus *Impatiens*, the Balsam, which is one of the characteristic genera of the Indian flora, occurring in all the hilly regions in great profusion, and each group of hills being principally occupied by species confined to that group, or endemic to it. They are herbs with watery translucent stems, alternate exstipulate leaves, and ☿ zygomorphic flowers. The **calyx** consists of five sepals, which are petaloid, and usually very irregular, the posterior one being prolonged into a large spur, the two anterior ones often small or even absent; the **corolla** is of 5 petals, those at the sides being united in pairs. The **stamens** are 5 in number, and their anthers are united in such a way as to form a kind of cap over the ovary, and, as the latter grows, the stamens break at the base and the whole cap falls off. The **ovary** is of 5 carpels, with 5 loculi and ∞ ovules, ripening to a capsule. This capsule is explosive, it is turgid when ripe in such a way that each of the segments into which it ultimately breaks is trying to roll up inwards, and when it finally snaps each one does so with a jerk, throwing out the seeds.

§ 24. Malvaceæ.

Distinguishing characters.—Herbs, shrubs, and trees; leaves alternate, stipulate; flowers solitary or in cymes, ☿, regular, hypogynous, usually 5-merous, and often with an epicalyx; calyx valvate, free or united, corolla convolute, stamens usually ∞ owing to branching, united into a tube, ovary (1—∞), most often (5), multilocular, with 1—∞ ovules in each loculus on axile placentæ; fruit usually a capsule or schizocarp.

This order is everywhere represented by the Shoe-flower (*Hibiscus Rosa-sinensis*) in gardens, and by the cotton (*Gossypium arboreum, herbaceum,* etc.) in fields, as well as by many common weeds, etc. They are herbs, shrubs, or

trees, the leaves alternate and stipulate, the flowers either solitary or in compound cymes

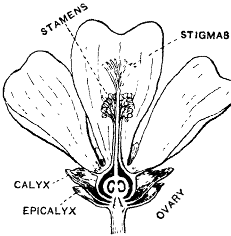


FIG 195 —VERTICAL SECTION OF FLOWER OF SPECIES OF *Hibiscus*

The **flower** (Fig. 195) is ♀, regular, hypogynous, 5-merous. Below the calyx there is very often an *epicalyx* present, which has sometimes been looked upon as of stipular nature, but as its numbers very often do not correspond with those of the calyx, it is perhaps more probably of bracteole nature. The **calyx** is 5 or (5), valvate, the corolla 5, convolute, with the petals usually asymmetrical, the **stamens** are generally indefinite, the inner whorl being branched, and are united below into a tube which is joined at the base to the petals, making the flower seem almost sympetalous; the anthers are monothecous, containing only two cavities instead of four, the **ovary** is of (1—∞) carpels, most often (5), multilocular with axile placentæ, the carpels being



FIG. 196.—CARCERULUS OF MALVACEÆ.

sometimes divided by transverse walls. The ovules are 1—∞ in each carpel, anatropous, usually ascending, the **fruit** (Fig 196) is generally dry, a capsule or a schizocarp (carcerulus), with one or many seeds, each containing an embryo which is curved in the endosperm

The flower is in general protandrous, when it opens the stamens are spread out and open, afterwards shrivelling and exposing the now ripe stigmas.

Most of the familiar plants of this order in India are garden plants, such as *Hibiscus Rosa-sinensis*, the Shoe-flower, so called from the use of the petals in polishing shoes; they are also used in colouring stewed mangoes and other fruits, and for other purposes This plant is very variable, and also lends itself readily to hybridisation with *H schizopetalus* and other species, and a large number of cultivated forms are known Several other species of *Hibiscus* are also in cultivation, such as *H. Sabdariffa*, the Rozelle, whose calyx becomes fleshy round the fruit, with a pleasant acid taste, which causes it to be largely used for jellies and other purposes, *H esculentus*, whose half ripe fruits, Bhindi (Lady's Finger), are very slimy when cooked and are largely used as vegetables and in soups, *H tiliaceus*, common on the sea coast, whose bark yields a very strong fibre, *H cannabinus*, often cultivated for the sake of the fibre of the bark, etc Many Abutilons are also cultivated, as well as *Althæa rosea*, the Hollyhock (Gulkhaira), *Thespesia populnea*, the Tulip-tree of the English, and others, while there are many species of *Sida*, *Urena*, and other genera among the commonest weeds, many of these yield good fibre Several of the family are important in cultivation, more especially the Cotton (*Gossypium*), of which several species are cultivated in India, *G. herbaceum* being generally regarded as the most common, whilst *G. arboreum*, the Tree Cotton, is everywhere grown in small numbers. *Eriodendron anfractuosum*,* a small tree with horizontally spreading branches, is the Silk-cotton or Kapok, the silky cotton is not, as in *Gossypium*, an outgrowth of the testa, but of the inner wall of the capsule, becoming separated from this when ripe, it is largely used for stuffing pillows. The similar cotton of *Bombax malabaricum*, the Cotton tree (the Shálmalí of the Sanskrit writers), is sometimes used, but rarely, being so high above the ground that it is difficult to reach. This tree is a very striking feature in any landscape where it occurs, in the months of December, when it loses its foliage, and January, when it bursts into a blaze of scarlet flowers upon the naked branches The ripe seeds, surrounded by the

* This and *Bombax* and *Adansonia* are usually placed in a separate family, Bombacaceæ.

cotton, fall, sometimes almost like a shower of snow, in April, when the young leaves are coming out *Adansonia digitata*, the Baobab, is another tree of this family that is to be found in a few localities, where it is supposed to have been introduced from Africa by the west coast Mohammedans; it has a short but very thick swollen stem, sometimes reaching as much as 20 feet in thickness and more or less egg-shaped, in which it stores up enough water to last over the worst droughts. The seeds are about 30 in a pouch-like fruit, which is often known as Judas' bag, it is woody, and contains a pulp in which the seeds are embedded

§ 25. Dilleniaceæ.

Distinguishing characters:—Trees and shrubs, often climbing; leaves alternate, usually leathery; flowers ☿, *in cymes, hypogynous; calyx* 5, *sometimes* 3, 4, or ∞, *spirally arranged, persistent on the fruit; corolla usually* 5; *stamens* ∞, *hypogynous, free or united below; carpels* ∞—1, *free or more or less united, with* ∞—1 *ovules, fruit of follicles, or fleshy; seed with a funicular aril, and endosperm.*

This is a small tropical order, mostly represented in the scrub vegetation of northern Australia, but with a few common plants in India. Most are trees and shrubs, sometimes climbing, with alternate, usually leathery leaves, and cymes of flowers.

The **flowers** are ☿, with spirally arranged persistent calyx, most often of 5, but also of 3, 4, or ∞ sepals, the corolla is usually 5, the stamens ∞, hypogynous, free or united at the base, the carpels ∞—1, free or more or less united, the styles usually free. The ovules are ∞—1, erect, anatropous, with ventral raphe. The **seed** has a funicular aril attached to the testa, and the embryo is small in copious endosperm.

Dillenia indica is perhaps the commonest species; it is a tree with large white flowers, which are succeeded by large apple-like fruits (Chaltá). The fruit is capsular and enclosed in the greatly enlarged and succulent sepals, which are edible. When cut, the fruit gives a lather with water, and is used in washing, especially for the hair. Some of the Acrotremas, to be found in the south, are pretty little herbaceous plants and there are a few other species

§ 26. Dipterocarpaceæ.

Distinguishing characters.—Trees with entire stipulate leaves, and racemose inflorescences of ☿ regular hypogynous flowers, calyx and corolla 5, stamens 5, 10, 15, or more; ovary trilocular, fruit a nut, with persistent calyx, some of whose leaves grow out into wings

This is one of the characteristic orders of India, but needs only a brief mention, as the trees are very tall, and flower rarely, so that it is very difficult to obtain material for study. The **leaves** are stipulate and entire, and the **flowers** in racemose inflorescences, with the formula K5, C5, A5, 10, 15, or more, $\underline{G}$ (3), 3-locular, with two ovules in each. The **fruit** is generally a one-seeded nut, surrounded by the persistent calyx, some of the sepals of which, usually two (whence the name of the order), grow out into wings. The trees are common in the forests of India, and many of them yield valuable timber, especially *Shorea robusta*, the Sal, and species of *Dipterocarpus*, many also furnish useful resins or gum-resins.

[§ 27 **Caricaceæ.**—This order is not indigenous to India, but is everywhere represented by the cultivated papaws, which were placed in Passifloraceæ in the older classifications. They are natives of South America and the West Indies, but were early introduced to the East by the Portuguese. They have a very characteristic habit, with tall erect stem crowned by a tuft of leaves, something like a palm The leaves and the unripe fruit contain the proteid ferment papain, and if meat be buried with the leaves wrapped round it, or still better rubbed with the juice of the unripe fruit, a partial digestion will take place, rendering the meat more tender The **flowers** are unisexual, hypogynous, regular K5, C(5), A5 + 5, $\underline{G}$5 with one or five loculi and ∞ anatropous ovules The **fruit** is a large fleshy berry, resembling a melon, and in most species, especially *Carica Papaya*, the common Papaw (Papayá), is edible and much appreciated]

§ 28 **Cactaceæ.**

Distinguishing characters.—*Fleshy plants with usually tufts of thorns and no leaves, flowers usually solitary and ☿; perianth ∞, with gradual transition from sepals to petals, stamens ∞, ovary inferior, unilocular, with ∞ ovules on parietal placentæ, fruit a berry.*

This order is represented only in Ceylon, in a truly native condition, by the epiphytic *Rhipsalis Cassytha*; but certain Opuntias or prickly pears are everywhere common in the East, especially in dry places and on the sea beach. The family shows on the whole the most pronounced xerophytism to be found, for not only is the surface exposed to the air greatly reduced, and the cuticle thick, but also a large amount of water is stored up in the fleshy tissues

In the Opuntias the stems are flattened, and each successive joint grows out as a branch on the one which preceded it The surface is generally covered with little groups of spines, arranged according to a definite phyllotaxy, these are in reality the leaves of the axillary shoot due to appear at this point. The leaves of *Opuntia* appear early, and are small, whilst they only function for a very short time in most species, and drop off, leaving the fleshy green stem to do most of the work of assimilation for the plant. In many of the Cacti, the stem is angular, and looks exactly like that of one of the large fleshy Euphorbias that are so common in India, but the cactus stem bears its thorns in little groups, the Euphorbia in pairs

The **flowers** are usually solitary, ☿, regular or irregular, and generally large and brightly coloured. The floral organs are most commonly all ∞, the sepals showing a gradual transition into petals; the **ovary** is unilocular with ∞ ovules on parietal placentæ, and a simple style; the **fruit** is a berry, with the flesh formed by the growth of the stalks of the ovules It is often edible, though care must be taken to avoid the thorns

§ 29. Myrtaceæ.

Distinguishing characters:—Trees and shrubs with oil glands in the leaves, which are usually opposite, exstipulate, entire, flowers ☿, *regular, in cymes, epigynous; calyx* 4-5, *often united, sometimes thrown off as a lid, corolla* 4-5, *sometimes thrown off also; stamens* ∝ *usually bent down inwards in bud; ovary inferior, with* ∝—1 *loculi and axile placentas, each with* 2—∝ *ovules, and simple style and stigma; fruit a berry, drupe, capsule, or nut, seed exalbuminous.*

This is a large order, well represented in the tropics, especially among the cultivated plants, which include the Jambulams, Guavas, Eucalypti, etc. They are trees and shrubs, sometimes climbing, and have usually oil glands in the leaves which may be recognised by holding them up to the light, when the glands show as little clear spots. The leaves are generally opposite, exstipulate, evergreen and entire There is often a so-called infra-marginal vein.

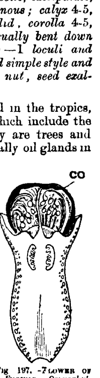


FIG. 197.—FLOWER OF *Eugenia Caryophyllata* (CLOVE). AFTER WARMING.
CO, Calyptra.

The **flowers** are usually in cymes, regular, ☿, the receptacle hollow and united to the ovary, the flower being in consequence epigynous. The **calyx** is (4-5) or 4-5, and is sometimes thrown off as a cap on the opening of the flower, instead of opening in the ordinary way; the **corolla** is also 4-5, the petals often nearly circular, and sometimes thrown off bodily as a cap on opening, the **stamens** are ∝, free, usually bent inwards in the bud, the **ovary** is syncarpous and inferior, with ∝—1 loculi, with 2—∝ anatropous or campylotropous ovules in each, the style and stigma simple, the placenta usually axile. The **fruit** is a berry, drupe, nut or capsule, containing exalbuminous seeds.

Among the native or cultivated forms in India are the various Jambulams, some native, some of Malayan origin, all species of

Eugenia, with fleshy fruits, which are edible, though not specially attractive Among them are *E malaccensis*, the Malay Apple, *E Jambos*, the Jambu or Rose-apple, the South American *E Michelii*, the Brazil Cherry, and many others. *Eugenia caryophyllata*, a Malayan species, furnishes the cloves of commerce (Lavang), which are the dried flower buds (Fig 197) The genus *Eugenia* is very characteristic of the flora of the hills of southern India and Ceylon, occurring in each group of hills in very many species, the Ceylon mountains for example possessing 43, of which 29 are endemic, or confined solely to that group of hills

Rhodomyrtus tomentosa, the Hill Guava, or Hill Gooseberry, is another very common plant along the edges of patches of forest in the hills. The various Guavas proper are species of *Psidium*, mainly introduced from tropical America by the Portuguese, the commonest, now a troublesome weed on much waste ground, is *P Guayava*, the Guava par excellence, which makes an excellent jelly Various species of *Barringtonia* are common along the coasts, where they form small trees Among the best known plants of this family, to those who visit the hills, are the various species of *Eucalyptus* which are so much planted there, but which are really natives of Australia, where they form a very characteristic feature in the landscape The best known of them is perhaps *E Globulus*, the Blue Gum, which in the younger parts has bluish-coloured opposite leaves on square branches, while in the older parts it has greenish alternate leaves on round branches Among the important species cultivated are *E Leucoxylon*, the Ironbark, *E robusta*, the Swamp Mahogany, *E marginata*, the Jarrah (which yields the very resistent timber now so much employed in paving the streets of London), and others Many of the gum trees, as the Eucalypti are commonly called, yield a valuable timber, others give kino (see under Leguminosæ), and several yield the well-known Eucalyptus oil by distillation of the leaves

§ 30 Umbelliferæ.

Distinguishing characters —Flowers polypetalous, epigynous, pentamerous, 5 stamens, structure of ovary and fruit

This is a very large and important order, easily recognised by the general habit of the plants and their fruits The plants are either herbs or shrubs with hollow (fistular) stems and alternate, amplexicaul, exstipulate leaves, which are usually much divided

The **inflorescence** is usually a compound umbel (Fig 153), occasionally a simple umbel. These umbels are

sometimes cymose in character, and a terminal flower may occur as in the Carrot (*Daucus Carota*). The **flowers** (Fig 135) are usually hermaphrodite and regular; but unisexual flowers sometimes are found, and frequently the outer flowers of the umbel are irregular and zygomorphic

The **calyx** is small, consisting of five minute sepals, or absent. The **corolla** is polypetalous, the five petals are usually white or yellow, and often have reflexed tips. The **stamens** are five in number and epigynous The **gynæceum** (Fig. 135) is bicarpellary, syncarpous; on top of the ovary is a honey disc surrounding the two stigmas; the *ovary* is bilocular with one suspended ovule in each loculus The **fruit** is a cremocarp (Fig. 168). Each mericarp is usually marked by five longitudinal ridges (*costæ*) containing vascular bundles, between the ridges are furrows (*valleculæ*) under which there are oil-ducts (*vittæ*). Secondary ridges and vittæ are frequently present between the primary ones. The **seed** is albuminous; the food-material consists of proteids and oils

Pollination.—The flowers are markedly protandrous, and, the honey secreted by the epigynous honey-disc being easily accessible, are visited by many short-tongued insects, especially flies and beetles

Floral formula —K5 or 0 C5 A5 $G(\overline{2})$

The order itself is easily recognised; but, in order to distinguish with accuracy the numerous genera, careful examination of the ripe fruits is often necessary.

In India this order is best known because of the cultivated plants which are commonly used all over India to flavour dishes. *Fœniculum vulgare* (Saunf), Fennel, *Coriandrum sativum* (Dhania), Coriander; *Cuminum cyminum* (Zírá), Cumin seeds. *Daucus Carota* is the Carrot (Gájar).

The wild Umbelliferæ are mostly found in the hills, and include species of *Bupleurum*, with *undivided*, ovate, lanceolate or linear leaves, *Heracleum*, *Selinum*, *Chaerophyllum*, etc. A few occur at alpine altitudes, and possess a strong smell which is said to promote mountain-sickness

CHAPTER XIV.

CLASSIFICATION OF ANGIOSPERMS NATURAL ORDERS—*Continued*.

B SYMPETALÆ. Perianth in two whorls ; corolla, with few exceptions, gamopetalous, stamens twice as many as the petals, or as many, or reduced to 4 or 2, epipetalous except in Ericaceæ and Campanulaceæ

SYMPETALÆ

§ 1. Ericaceæ.

Distinguishing characters :—Flowers gamopetalous, hypogynous, epigynous in Vaccinium ; pentamerous or tetramerous, stamens usually twice as many as the sepals and petals, and not epipetalous ; anthers often with appendages and opening by apical pores, pollen in tetrads ; placentation axile Shrubby plants growing usually on moors and hills

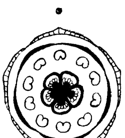


FIG 108.—FLORAL DIAGRAM OF RHODODENDRON

In northern Europe the Ericaceæ form a dominant family upon the heaths and moors which abound there, in India this is not the case, except to some extent in the Himalaya, where the Rhododendrons form a very striking feature in the flora of some districts at high elevations. Owing to the situations in which they grow, these plants usually show more or less marked xerophytism The Rhododendrons generally form true winter buds, which are rare in tropical plants. The leaves are usually entire, leathery, with a thick cuticle.

The **inflorescence** is usually racemose with ☿, regular or slightly irregular **flowers**, which have a calyx of 4-5 sepals, a *corolla* of 4-5 united petals, 8-10 *stamens*, of which the outer whorl is opposite to the petals, and not as usual alternating with them, this condition is termed *obdiplostemony*, and occurs in a number of orders All these organs are hypogynous, and the **ovary** is superior, of (4-5) carpels. But in the sub-order Vaccinioideæ, of which a few members are to be met with among the hills, chiefly as epiphytic growths, the ovary is inferior, and the other parts epigynous. The **fruit** is a capsule, drupe, or berry

The anthers open by pores, and the last division of the pollen mother cells is not complete, so that the four pollen grains formed by it do not separate, but remain attached in what is termed a *tetrad*. The pollen is very powdery, and pours out of the pore at the tip of the anther upon the head of a visitor

Rhododendron, *Vaccinium*, and *Gaultheria* are the only common members of the family in India.

§ 2 Myrsinaceæ.

Distinguishing characters :—Shrubs and trees with alternate, entire, exstipulate leaves, and flowers in racemes, calyx and corolla 5, united, stamens 5, epipetalous, opposite to petals; ovary unilocular, with basal or free-central placenta, fruit a drupe

This is a family of moderate size, represented in the tropics by a great many species of *Ardisia* and other genera They are mostly shrubs and trees with alternate leaves, which have no stipules, and racemes or panicles of flowers, ☿ or unisexual, regular, with the formula usually K(5), C(5), A5, but opposite to the petals and not alternating with them, $\underline{G}$ unilocular, with simple style and few or many ovules on a basal or a free-central placenta, the latter being one which stands up into the middle of the ovary. Fruit a drupe

Ardisia, *Mæsa*, *Embelia* are frequent in India, and *Ægiceras* is one of the mangroves

§ 3. **Apocynaceæ.**

Distinguishing characters :—Twining or erect herbs, shrubs, or trees; leaves usually opposite, entire; latex present; flowers ☿, *regular, calyx 5 united, corolla 5 united, convolute; stamens 5, epipetalous, carpels (2), superior or 2 united by style only, fruit of two follicles or a berry, seeds often with tuft of hairs*

This is a fairly large order, chiefly tropical, and well represented in India by many common weeds, and by the Oleander and the Temple Tree, introductions from abroad. Most of them are twining shrubs, but many are erect herbs, shrubs, or trees The leaves are most commonly opposite, simple, and entire, and there is always latex in the stem

The **inflorescence** is a panicle, but sometimes has more or less of cymose branching, the **flowers** are regular and ☿, with the formula K(5), C(5), A(5), epipetalous, G (2), or very often the carpels are free below and united above by the style only The **fruit** is a berry or, more commonly, a very characteristic fruit of two follicles, the seeds in which are often flat, and have a tuft of long fine hair at one end which serves to distribute them to a distance.

The most familiar members of this order in India are probably the Oleander (*Nerium Oleander*, Kaner) and the Temple Tree (*Plumeria acutifolia*), both of which are introductions, the former from Persia, the latter perhaps from tropical America. There are many common plants of this order in India, but none of great interest or importance

§ 4. **Convolvulaceæ.**

Distinguishing characters —Herbs or shrubs, often climbing, sometimes parasitic, with alternate, seldom stipulate leaves, inflorescence of ☿ *regular hypogynous flowers in cymes, calyx usually 5, corolla (5), stamens 5, alternate with the petals, epipetalous, ovary on a disc, usually (2), bilocular with axile placentæ and usually two ovules in each loculus, fruit a berry, nut, or capsule, with albuminous seeds*

This order is well represented in India by many species of *Ipomœa*, which are often cultivated for ornamental pur-

poses. Many of the family, *e.g* most of the Ipomœas, are climbers with twining stems, others are erect herbs or shrubs, some are thorny xerophytes, and one, *Cuscuta*, is a twining parasite (p. 196). Some, *e g.* the Sweet Potato (*Ipomœa Batatas*, Shakarkand), have tuberous roots, and many of them have latex. The leaves are alternate, usually stalked, exstipulate, and the inflorescence is cymose.

The **flowers** are ☿, regular, hypogynous, and 5-merous. The **calyx** is 5, imbricate, with the odd sepal posterior, the **corolla** (5), infundibuliform, the petals often so completely united that there are no free ends to the petals, the **stamens** 5, epipetalous and introrse, the **ovary** (2), on a honey-secreting disc, with axile placenta, and 2 or rarely 4 ovules in each loculus erect, and anatropous. The **fruit** is a berry, nut, or capsule with albuminous seeds.

The best known genus is *Ipomœa*, of which there are very many species with elegant trumpet-shaped flowers. One of the most interesting is *I biloba*, which forms a characteristic feature of the flora of the sandy beaches of the eastern tropics; it has long creeping stems, which root at the nodes, somewhat fleshy xerophytic leaves, and handsome purple flowers Another well-known one is *I Bona-nox*, the Moon-flower, which opens in the evening and fades the next morning, and there are many cultivated and wild Ipomœas Among the former is *I Batatas*, the Sweet Potato, introduced from tropical America, with tuberous swollen roots The little blue-flowered *Evolvulus* is common in waste places *Cuscuta*, the Dodder, is common in some parts of India in several species, which have been elsewhere described. *Convolvulus arvensis* is a common weed all over India

§ 5. Labiatæ.

Distinguishing characters:—Flowers gamopetalous, hypogynous, zygomorphic, stamens didynamous and epipetalous, fruit a carcerulus. The square stems, opposite decussate leaves, inflorescence, and bilabiate ringent corolla are characteristic.

This is an important order, consisting of herbs or undershrubs with square stems and opposite decussate, simple, exstipulate leaves Most of them are land-plants; a few are marsh-plants. Suckers are found in many forms (Fig. 50) In most of them there are numerous epidermal

glands (glandular hairs) secreting volatile oil. Well-known examples are the Dead-nettles (*Lamium*), Thyme

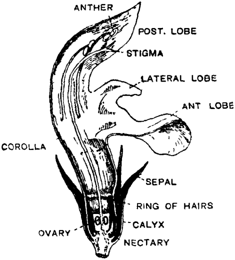


FIG 199.—VERTICAL SECTION OF FLOWER OF WHITE DEAD-NETTLE.

(*Thymus*), Lavender (*Lavandula*), Mint (*Mentha*), Ground Ivy (*Nepeta*).

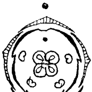


FIG 200.—FLORAL DIAGRAM OF LABIATÆ

The characteristic **inflorescence** is the verticillaster (Fig 154, p. 254). The **flowers** (Figs 199, 200) are hermaphrodite, zygomorphic, and pentamerous, with suppression of certain parts. The **calyx** is gamosepalous, tubular, funnel-shaped, or bilabiate, persistent The **corolla** is zygomorphic, bilabiate ringent; sometimes, as in Mint, it is almost regular. The **stamens**, owing to the suppression of a fifth (the posterior one), are four in number, epipetalous and didynamous, occasionally there are only *two stamens*.

The **gynæceum** is bicarpellary and syncarpous Early in its development a median constriction appears in the ovary and produces two false septa The style is *gynobasic*, *i e* it arises from the base and comes up from between the four parts of the ovary, this is not the case, however, in the Bugle (*Ajuga*) and Wood Sage (*Teucrium*). There is a bifid stigma The ovary is quadrilocular (two true and two false septa) with one erect anatropous ovule in each loculus The placentation is axile. The **fruit** is a carcerulus (p. 280). The **seed** is exalbuminous

In some species, *e g* Thyme, Ground Ivy, and Self-heal, female flowers occur, usually on different plants from those with the ordinary hermaphrodite flowers. This is known as **gynodiœcism** It promotes cross-pollination

Pollination.—There is a honey disc at the base of the ovary, best developed on the anterior side (Fig 199) Usually the flowers are protandrous In many cases, after the anthers have opened, the stamens move outwards or downwards, and the style moves into their place. When the flowers are homogamous, as in the Dead-nettle, the style projects below the anthers so as to be touched first by the visiting insect Self-pollination, however, may take place.

In the short-tubed flowers of Mint and Thyme, with more or less regular corolla and spreading stamens, all sorts of insects crawl over the flowers and touch the anthers and stigmas with any part of their bodies Most Labiates, however, have a conspicuous lower corolla-lip to attract insects and to act as a landing place, and usually an arched upper lip to shelter the stamens and style, which are generally placed so as to touch the insect's back as it enters the flower Small insects may be excluded, as in the White Dead-nettle, by the narrowing of the lower part of the corolla-tube and the development of a ring of hairs The mechanism in *Salvia* is described on p 264

This order is represented in the Temperate Himalaya by a very large number of species belonging to the genera *Mentha*, *Salvia*, *Plectranthus*, *Lamium* and many others, some of which are also found in the plains. The two best known Indian Labiatæ are *Mentha* (Pudíná), Mint, and *Ocimum sanctum* (Tulsí).

§ 6. Solanaceæ.

Distinguishing characters:—Flowers gamopetalous, hypogynous, regular and pentamerous, stamens 5, epipetalous, sometimes syngenesious, pistil bicarpellary, syncarpous; fruit a capsule or berry.

This order is well represented in tropical countries, but only a few genera are found in Europe It consists of herbs, shrubs, and trees, with simple, more or less divided, exstipulate leaves, which are alternate in the vegetative

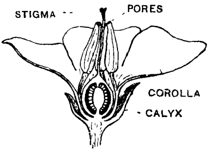


FIG 201 —VERTICAL SECTION OF FLOWER OF *Solanum*

region, but sometimes appear in pairs in the region of inflorescence

Very often, in the region of inflorescence, adnation of the bracts to the axillary branches occurs, so that at any one node the two leaves that occur are seldom either opposite or equal

The **inflorescence** is usually a cyme The **flowers** (Figs. 201, 202) are regular, or nearly regular, pentamerous, and hermaphrodite.

The **calyx** is gamosepalous, five-cleft, and persistent; in the Cape Gooseberry (*Physalis*), for example, it forms the bladder-like investment to the fruit The **corolla** is usually rotate or campanulate. The **stamens** are five in number, epipetalous, and alternate with the lobes of the corolla The anthers are sometimes connate (syngene-

sious, e g *Solanum*), and dehisce either by longitudinal slits or by pores (*Solanum*).

The **gynæceum** is bicarpellary and syncarpous, the *ovary* usually bilocular, but it sometimes becomes multilocular owing to the formation of false septa (*Datura*) The two carpels are placed obliquely in the flower and not in the median plane (Fig 202). The **placentas** are axile, usually large and swollen, and bear numerous ovules. The *style* is single; the *stigma* simple or bilobed

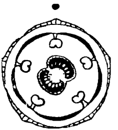


Fig 202 —FLORAL DIAGRAM OF *Solanum*

The **fruit** is a capsule (*Datura*) or berry (*Solanum*). The **seed** is albuminous The flowers are entomophilous. *Nicotiana* is pollinated in the evening by moths

The Solanaceæ are closely allied to the Scrophulariaceæ. They are distinguished from the latter by their regular or nearly regular flowers, and by the oblique position of the carpels (a character, however, not easily recognised)

Floral formula —$\mathbf{K}(5)\ \widehat{C(5)\ A5}\ C(\underline{2})$

India contains many species of Solanum (including *S. tuberosum*, the Potato) and *Datura* (including the introduced Trumpet Flower, *D suaveolens*) Chillies and bird-pepper (species of *Capsicum*), the Tomato (*Lycopersicum esculentum*), and others are largely cultivated *Solanum nigrum* is the Black Nightshade, found throughout India, *Hyoscyamus niger*, the Henbane, and *Atropa Belladonna*, the Deadly Nightshade or Belladonna, both grow in the N W. Himalaya

§ 7 Scrophulariaceæ.

Distinguishing characters :—Chiefly herbs, often climbing; leaves alternate or opposite, exstipulate; inflorescence racemose or cymose, ☿ *hypogynous zygomorphic flowers (nearly regular in Verbascum, etc); calyx (5), corolla (5), often strongly two-lipped, stamens epipetalous, 4, didynamous, or 2, rarely 5; ovary superior, of (2) carpels, with* ∞

ovules on axile placentas, and simple or bilobed style; fruit a capsule or berry with albuminous seeds

This is a large order better represented in the hills than in the plains, though Snapdragons and other members of it are often cultivated in the cold weather. Most are herbs or undershrubs, with alternate, opposite, or whorled exstipulate leaves. Some are climbers, e g. ***Maurandia***, a Mexican plant which has naturalised itself in some districts. Some are partial parasites, e g *Striga*, which

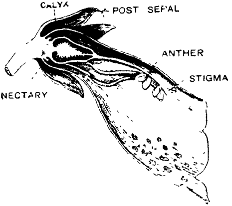


Fig 203 —L. Section of Flower of *Digitalis*.

grows on the roots of the cultivated Sorghums The inflorescence is a spike or raceme, or a cyme, which may be of complex construction

The **flower** (Figs 203, 204) is ☿, and zygomorphic, except in the introduced Verbascums and Veronicas, in which it is almost regular, especially in the former Most of the order show the type, which is well exhibited in the Snapdragons or in the Torenias, which are common in many districts The **calyx** is (5), the **corolla** (5), two-lipped, the **stamens** 4, two longer than the other two (didynamous), the posterior or missing stamen sometimes represented by a staminode, the **ovary** (2), bilocular with

axile placenta, ∝ anatropous ovules, and a simple or bilobed style. The **fruit** is a capsule or berry, surrounded by the persistent calyx, with ∝ small albuminous seeds.

In *Verbascum*, which is naturalised in the hills in some districts, the corolla is regular and there are 5 stamens, in *Veronica*, also naturalised in places, and native in the far north, the calyx and corolla are each 4, the posterior petals being united, the stamens 2, and the corolla rotate and nearly regular.



FIG. 201.—FLORAL DIAGRAM OF TYPICAL SCROPHULARIACEÆ. AFTER EICHLER.

There are several types of adaptation to the visits of insects which may cause **pollination.** In the Verbascums and Veronicas the flower stands widely open and is visited by almost any sort of insect, in the Torenias, Snapdragons and flowers of that construction, there is honey secreted by a disc below the ovary, and the flower is visited chiefly by bees, which touch the essential organs, these being against the back of the corolla, with their backs; as the stigma usually projects beyond the stamens this means as a rule that cross-fertilisation will occur. In the Strigas and similar flowers, lastly, there is what is often termed a "loose-pollen" mechanism, the pollen being loose and powdery, and lying in a box formed by the anthers, which have spine-like projections that may be jostled by an insect entering the flower, and cause him to receive a shower of pollen upon his head, while the stigmas project beyond the stamens, and get touched before them. In many Scrophulariaceæ (*Mimulus, Torenia*) the two lobes of the stigma come together if touched on the receptive surface.

Many of the order are officinal (e.g. *Digitalis*), and many are garden favourites. The most interesting and common of the native members of the family are *Striga*, which is parasitic upon the roots of Sorghums, and *Torenia*, which is a very popular garden plant. Among the species introduced to India are *Verbascum Thapsus*, the Mullein of Europe, *Calceolaria chelidonioides*, a Mexican

plant, with the lower lip of the flower expanded into a large yellow bag, *Antirrhinum majus*, the Snapdragon, and others Numerous species of *Pedicularis* are quite common in the Himalayas *Celsia coromandeliana*, with an almost regular corolla, grows in the plains and the lower hills of India.

§ 8. Acanthaceæ.

Distinguishing characters:—Shrubs and herbs; leaves opposite, exstipulate; inflorescence cymose, of ☿ hypogynous, irregular flowers, calyx (4-5), *corolla* (4-5), *usually two-lipped, stamens usually* 4 *or* 2, *epipetalous; ovary of* (2) *carpels, bilocular, with axile placentas, each with* 2—∞ *anatropous ovules, and long style with two stigmas; fruit a capsule loculicidal to the very base and usually stalked, with exalbuminous seeds.*

This is a very large order, well represented in India by many common plants, which show very various habit, some being climbers, some xerophytes, some shore plants Mostly they are herbs or shrubs, with opposite exstipulate leaves, which are usually entire

The **inflorescence** is a dichasial cyme with a tendency to become monochasial in the later branchings, and quite frequently the cyme is "condensed" in the axils of the leaves in such a way as to make a little apparent whorl of flowers, whose cymose nature can be readily recognised by the fact that the central flowers open first. These cymes themselves are almost necessarily in racemose order, and actual racemose inflorescences also occur The **bracts** and bracteoles are often large and coloured, the latter sometimes enclosing the flower and taking over to a greater or less extent the functions of a calyx

The **flower** is ☿, hypogynous, and strongly zygomorphic. The calyx is (4-5), the corolla (4-5), usually very strongly two-lipped, though sometimes, as in *Acanthus* itself, the upper lip is not developed, the stamens are rarely 5, but usually 4 or 2, epipetalous, often with the missing stamens represented by staminodes, the anthers often with one small lobe or with a long connective, or with both; the ovary is (2), bilocular with axile placenta, and ovules

2—∞ in each loculus in two rows, the style long with two stigmas

The **fruit** is a bilocular capsule usually more or less stalked, and loculicidal to the extreme base, with exalbuminous seeds. In most of the order the seeds have peculiar outgrowths (*jaculators*) from the stalks, which are sometimes of hooklike, sometimes of papillar shape (Fig. 205). These lignify and stiffen, and by bending into a more or less horizontal position press the fruit wall outwards until it bursts with a jerk and throws out the seeds In *Ruellia* and others the seeds have hairs upon the surface which swell up when wetted and may be of use in anchoring the seed to its place of germination

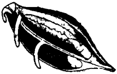


FIG 205—HALF OF FRUIT OF *Acanthus mollis*, SHOWING JACULATORS.

The flower secretes honey by a disc below the ovary, and by its size and complication is usually adapted to the visits of bees, while its mechanism is perhaps most commonly that which has been described under Scrophulariaceæ as the loose-pollen mechanism.

Among the more common of the family are *Thunbergia*, a small climbing (twining) plant with a much divided calyx *Ruellia*, mentioned above, *Barleria*, *Justicia*, *Adhatoda*, and other common weeds *Acanthus ilicifolius*, with its pretty flowers and prickly leaves, is common among the mangrove and swamp formations upon the coasts But perhaps the most interesting of the family is *Strobilanthes*, of which very many species grow in the forests upon the hills, and which forms one of the characteristic plants of the mountain flora, though a few species are occasionally found at low levels These plants form the undergrowth of the forests where they occur, almost to the exclusion of anything else They grow without flowering for several years, and then all flower simultaneously, the forest being then for a short time a sea of flowers, with innumerable bees at work among them, later the seeds are ripening, and the forest is full of jungle fowl feeding upon them; and finally there is nothing but a wilderness of dead sticks, until the young plants begin to appear and repeat the same history. Every mountain range, especially in the south, has numerous species of *Strobilanthes* confined to it, or *endemic* there, as it is called.

§ 9. **Rubiaceæ.**

Distinguishing characters:—Trees, shrubs, or herbs with decussate stipulate leaves and cymose inflorescence (in Galieæ the stipules as big as the leaves), flowers ☿, regular, epigynous, 4-5-merous, stamens 4-5, epipetalous; ovary usually bilocular, inferior; fruit usually capsular.

This is one of the largest orders of tropical plants, and represented in India by many native and cultivated plants; they are mostly trees and shrubs, but there are also a considerable number of herbs. The **leaves** are entire or very rarely notched, and are always stipulate. The **stipules** show great variety in form. Only comparatively rarely are there two stipules to a leaf, standing one on either side of it. Sometimes they are united in pairs, one of one leaf to the one of the other standing beside it (interpetiolar), sometimes they are united between the petiole and the stem (axillary), sometimes they are united to one another and to the leafstalks, so as to form a sheath round the stem, and in the tribe Galieæ, to which belong the Galiums and Rubias sometimes found in the hills, the stipules are large and leafy, exactly resembling the leaves, except that they have no axillary buds, and sometimes united in pairs, so that, with the leaves, a whorl of four is formed, sometimes free, forming a whorl of six.

The **inflorescence** is cymose, and in perhaps the majority of cases is a much branched cymose panicle, though small cymes are common. The **flower** is ☿, regular, and epigynous. The **calyx** is composed of 4 or 5 sepals, usually small, and sometimes almost unnoticeable, sometimes, as in *Mussænda*, one of the sepals is large and brightly coloured, forming the most conspicuous part of the flower and serving to attract insects. The **corolla** is of 4 or 5 petals, united, and in æstivation valvate, convolute, or imbricate. The **stamens** are also 4 or 5, alternating with the petals and epipetalous, and the **ovary** is inferior, of two or rarely of some other number of carpels, with as many loculi as carpels, *i.e.* most usually bilocular. The number of ovules in each loculus is either one—the distinguishing mark of the sub-order Coffeoideæ,

of which *Coffea*, the Coffee Plant, is a type—or more than one, most often very many—the distinguishing mark of the Cinchonoideæ, of which *Cinchona* is a type. The *style* is simple, with a head-like or lobed stigma. The **fruit** is most commonly a capsule, often a berry, less frequently a schizocarp, and the *seeds* have a large proportion of endosperm.

Among the more interesting members of the family to be found in India are *Oldenlandia*, a number of species of which are common weeds, especially on the seashore, and one of which, *O. umbellata*, the Chay-root, affords a dull pinkish purple dye from its roots, formerly much employed in India for dyeing cloths; *Hedyotis*, of which many species occur in the hills, the most interesting being *H verticillaris* of the Nilgiris and Ceylon, with a kind of basin formed by the broad expanded bases of the leaves, in which a considerable amount of water is collected and held, *Cinchona*, the source of the quinine and cinchonidine of commerce, originally a native of Peru, brought to India and Ceylon in 1861 by Sir Clements Markham, and now extensively cultivated by the Government in the Nilgiris and about Darjiling, the quinine obtained being sold only in India, where it may be obtained for a small sum at any post office; *Gardenia*, many species of which are native or cultivated in India, *Knoxia*, a common weed in the hills of the south, and showing heterostylism very well; *Coffea*, some species of which are native in India, but by far the best known of which is *C arabica*, the Arabian Coffee, largely cultivated in Mysore, *Ixora*, many species of which are to be found, some of them with very showy and handsome flowers, with long tubes preventing the honey being obtained by any but Lepidopterous insects, *Pavetta*, a shrubby species, of which several kinds occur, and which are marked by the presence of little pustules on the leaves, inhabited by colonies of bacteria, whose use or otherwise to the plant is entirely unknown; *Morinda*, some species of which are common on the seashore and elsewhere, and which have the flowers densely aggregated, with a certain amount of union of calices, etc, while the fruits are combined into one dense compound fruit; and many others. Many species of *Galium* and *Rubia* are common The roots of *R cordifolia* yield the red dye known as Manjeethh. *Nauclea Cadamba* (= *Anthocephalus Cadamba*) is the Kadam tree.

§ 10. **Cucurbitaceæ.**

Distinguishing characters:—Herbs climbing by tendrils; leaves alternate, flowers unisexual in inflorescences of different ***kinds; calyx and corolla*** *(5)* ***united; stamens***

sometimes 5, but usually less, most commonly 3, two large and one smaller, ovary inferior, 1-10-locular, most often 3-locular with 1—∝ ovules in each; fruit usually fleshy with exalbuminous seeds

This is a fairly large order, well represented in India by plants which are mostly climbing annuals, which grow rapidly and climb by aid of tendrils. About the morphological nature of these there has been much dispute, which cannot even yet be said to be finally settled, though the view which perhaps finds most favour is that the tendril is of dual nature, the lower part being stem, the upper leaf. The tendrils show nutation and the other phenomena of climbing very well indeed The leaves are alternate, often palmately notched

The **inflorescence** is of various types, the **flowers** itself unisexual, rarely ☿ The **calyx** is (5), the **corolla** (5), epigynous, regular, the **stamens** typically 5, but there is great variety in the andrœcium, which is usually zygomorphic, and has cohesions of various types. The anthers are always 2- not 4-locular. Only very rarely are there 5 stamens present, each with a bilocular anther In most of the family there appear to be 3 stamens, two of which have 4-locular anthers, in reality this is due to a fusion of two pairs of stamens, leaving the fifth free At the same time the anther loculi usually become much curved, and in some of the Pumpkins (*Cucurbita*) so much cultivated in India the pollen-sacs are remarkably twisted The **ovary** is inferior, with 1-10 most often 3 loculi, each containing 1—∝ anatropous ovules on axile placentæ, and with as many stigmas as carpels, though the stigmas are often forked The **fruit** is usually fleshy, of the type exhibited in the Pumpkin or the Cucumber—a berry-like fruit sometimes called a pepo, with exalbuminous seeds

Many of this family are cultivated on account of the edible fruit, e g *Trichosanthes Anguina*, the Snake Gourd, *Momordica charantia*, the Karela, *Lagenaria vulgaris*, the Bottle Gourd, *Citrullus vulgaris*, the Water Melon, an African species, *C. Colocynthis*, the Colocynth or Bitter Gourd, used in medicine, *Cucumis sativus*, the Cucumber, *C Melo*, the Melon, *Benincasa cerifera*, the Ash Pumpkin, *Cucurbita maxima*, the Gourd or Pumpkin, *C Pepo*, the Vegetable Marrow.

and other species, *Luffa ægyptiaca*, the Loofah or Bath Sponge, whose fruit contains a network of vascular bundles, which when set free by the rotting away of the softer tissue forms an excellent bath sponge, and many others of less interest.

§ 11. Compositæ.

Distinguishing characters:—Herbs or rarely shrubs or trees; leaves alternate or opposite, rarely stipulate; inflorescence racemose, the flowers in heads with involucres of bracts, the individual flowers of a head all actinomorphic (tubular), or all zygomorphic (ligulate), or both (forming disc and ray), the flowers epigynous; calyx absent or forming a pappus, corolla (5), *stamens* 5, *epipetalous, with coherent anthers, ovary inferior, of* (2) *carpels with two stigmas, and unilocular, with one basal ovule, fruit a cypsela, often with pappus, and with exalbuminous seed.*

This is the largest and most widely distributed order of flowering plants, and contains over 10,000 species. Although so large an order, the general characters of the Compositæ are so clearly marked that they cannot be taken for members of any other family, although there is at first glance a superficial resemblance to the members of the small closely allied order Dipsacaceæ.

Occurring as they do in every possible variety of situation, the plants of this family show every variety of habit, some being water or marsh plants, some climbers, some epiphytes All these types, however, are rare, and the great bulk of the order consists of moderate sized herbaceous plants, of which the Vernonias and Blumeas are excellent examples. Only rarely do shrubs of any serious size occur, the bulk of the Vernonias, for example, though many of them are more or less shrubby, not exceeding a couple of feet in height. The plants are mostly mesophytes, or suited to an average climate, but many grow in very dry situations, and have more or less fleshy leaves, or other protections against drought.

The plants have usually a tap root, which may in some cases, e g. *Elephantopus*, or the Dandelion (*Taraxacum officinale*, to be found in the hills), be tuberously thickened for storage of reserves. The leaves are usually radical

or alternate, often both types on the same plant, in rarer cases they are opposite, as in *Siegesbeckia*, and in the Sunflowers and Dahlias commonly cultivated in gardens; they are generally exstipulate. Oil ducts occur in most of the family, and latex is present in some, *e.g* the Dandelion and the Lettuce.

The **inflorescence** is in general a capitulum or head of flowers, of racemose type, as may be seen from the fact that the oldest flowers, which open first, are round the margin of the head (Fig. 151) The head is of symmetrical form, with a great number of, or sometimes only two or three, flowers on a common receptacle, surrounded and protected by an involucre of bracts, which may be in one whorl, or in several The disc or receptacle upon which the florets stand is commonly flattened or convex, and upon it are very often bracts to the individual florets, called *paleæ*, usually of chaffy nature. This capitular inflorescence is usually in common speech termed the flower of a Composite, as for instance the flower of a sunflower or dandelion, but in reality is a whole inflorescence condensed to resemble a single flower, the heads may of course be themselves arranged into more complicated inflorescences, such as spikes, racemes, or panicles

The **distribution of sexes,** and the form of the individual flowers, show great variety (Fig. 124, A, D). The simplest case is for all the flowers of a head to be ☿ and regular—or *tubular*, as it is termed But very often the outer florets of a head, as in the Sunflower, are irregular, strap-shaped, or *ligulate*, the flat petal into which the corolla is drawn out usually showing a number of notches at the end corresponding to the petals of which it is really composed. Most commonly, perhaps, the ligulate flowers are female, except when, as often happens, the whole head is made up of ligulate flowers. When, as in the Sunflower, there are central tubular flowers, they form what is called the *disc*, which usually differs in colour from the *ray* formed by the ligulate flowers round the edge of the head A few of the family have neuter regular flowers, of different size and form, at the edge of the head (*Centaurea* spp.).

The **florets**, or flowers themselves, are epigynous and 5-merous (Fig 206), and may be actinomorphic or zygomorphic, ☿, unisexual or neuter. Owing to the fact that the function of protection of the young flowers from the weather and other evil influences is taken over by the involucre of bracts on the head, the calyx of the individual flowers is thus rendered useless, and in fact a green leafy calyx is not found. In some cases it is simply aborted, appearing only as a slightly lobed rim on the summit of the ovary, but in the great majority of the Compositæ the plant has, so to speak, been able to find another use for it, and it appears in the form of a **pappus**—a ring of small hairs or bristles, which after fertilisation enlarges into a parachute of fine hairs by means of which the fruit may be carried to a long distance from the parent plant, or into two or more stiff barbed bristles, by whose means the fruit may cling to animals and thus be distributed to a distance.



Fig. 206.—Floral Diagram of Compositæ, with Pappus (after Eichler).
The small outer lines represent the pappus bristles

The **corolla** is (5), and in bud the petals are valvate; it may be actinomorphic or zygomorphic, the former giving the tubular flowers of which we have already spoken, the latter usually the ligulate, though sometimes the flowers are merely labiate or lipped. The **stamens** are 5, epipetalous, with short filaments, and alternating with the petals, the anthers are introrse, and cohere with one another by their edges, and form a tube around the style (Fig 124, A). This form of cohesion is described by the term *syngenesious*. The **ovary** (Fig. 136) is inferior, of (2) carpels, with a simple style that forks at the end into two stigmas, of which one is posterior, the other anterior; it is unilocular, with one erect, basally attached, anatropous ovule which after fertilisation gives rise to an exalbuminous seed with a straight embryo, enclosed in a dry indehiscent pericarp, the whole being popularly termed the seed, though it is really the fruit. The **fruit** is usually called an achene,

but is of course of more than one carpel, and its wall is partly of axial nature, and is more strictly to be called a cypsela (Fig. 162, A). When present, the pappus crowns the fruit.

The mechanism of **pollination** is interesting and simple, and shows much the same general features throughout the family. The florets are in general small, and closely massed together, which makes the inflorescence attractive to insects, moreover an insect can visit a great many in a very short time. Honey is secreted by a ring-shaped nectary at the base of the style, and is well protected from rain and from insects with short lips by the longish narrow tube of the corolla which stands above it. The actual length of the tube varies very much, but there is always a tube of sufficient length to keep out the smaller and more stupid insects In general it is longer in the blue coloured species, which are favourites with bees and butterflies, than in the yellow coloured species, which are more visited by the larger and more intelligent flies

When the flower opens, the style, with its stigmas close together, so that the receptive parts are completely covered, reaches up to the bottom of the tube formed by the anthers, which open and shed their pollen. This is then pushed outwards by the growing style, and the flower is in its male stage, while ultimately the pollen is all pushed out, and the styles emerge and open their stigmas to expose the receptive surfaces, and the female stage begins. Ultimately, in a great majority of cases, the stigmas curl round backwards so far as to touch the pollen that may still be upon their backs, and self-pollination occurs, so that the flower will set seed in any case, while getting a chance of setting cross-fertilised seed as long as possible. This simple and effective mechanism should be carefully contrasted with that of the orchids, where there are large and complicated flowers which yet so rarely effect their object that they have to set a vast number of seeds, whereas in the Compositæ there are simple flowers which are so efficient that one seed is sufficient.

The ripening fruit, like the young flower, is protected by the involucre of the head, and, as already mentioned,

the calices of the individual flowers most often form a pappus, which aids in the distribution of the seeds.

The Compositæ are generally regarded as occupying the highest position in the vegetable kingdom, and this may be put down to the fact that they possess several very efficient peculiarities, viz. (1) the massing of the flowers in heads, which gives greater conspicuousness, especially in cases where rays of ligulate flowers are formed, and a saving of material in the construction of corollas, for the individual flowers may be much smaller, and one insect, walking over the head, can pollinate many flowers in a short time, (2) the very effective and extremely simple mechanism of the flower, giving good protection to the honey and pollen, excluding the most stupid insects, but leaving the flowers available to a large circle of visitors, preventing self-pollination till the last possible moment, but giving it at last, and thus ensuring the setting of seed, and (3) the use of the calyx of the individual flower to form a very perfect mechanism for the distribution of the seeds In all these respects the Compositæ should be carefully compared with the other orders dealt with in this book

There are a very great number of Compositæ in India, though not so many in proportion to the rest of the flora as one finds in more temperate countries Among the more prominent are the many species of *Vernonia*, some of which are among the commonest weeds, and some of which are large and shrubby, *Elephantopus scaber*, one of the commonest weeds in lawns and grass land, with its large leaves which lie flat on the ground, and its tuberous root, which enables it to come up again, if cut off, by the aid of the reserve that it contains, *Carthamus tinctorius*, the Kusum, many Blumeas, often with rather woolly leaves, the many species of *Anaphalis* of the hills, which with their white woolly leaves resemble the Edelweiss of Switzerland, to which they are somewhat closely related, *Xanthium Strumarium*, which has two forms of head—one male, one female: the former at the outer ends of the inflorescence, the latter lower, with two apetalous flowers enclosed in an involucre of united bracts, only the styles projecting out of the two cavities in the involucre, and the latter provided with hooks by whose means the fruits may be distributed, *Bidens pilosa*, the Spanish Needle, with the achene provided with barbed hooks at the outer end; several Senecios, some of which climb by twining, *Launæa pinnatifida*, which is very common on the sea beach and grows by

runners that take root at the nodes; *Cichorium Intybus*, the Wild Chicory.

Among the introduced plants, which are often among the commonest weeds, are *Ageratum conyzoides*, the Goat-weed, from tropical America; *Tithonia diversifolia*, the Wild Sunflower (Mexico), *Helianthus annuus*, the true Sunflower, whose fruits yield an oil, *Helianthus tuberosus*, the Jerusalem Artichoke (the name Jerusalem is really the Italian *girasole*, meaning turning to the sun, for the flower heads tend to face the sun); the pretty yellow species of *Cosmos* from Mexico; *Cynara Cardunculus*, the true Artichoke, the edible part of which is the lower inner edges of the involucral bracts, *Taraxacum officinale*, the Dandelion, *Lactuca scariola*, the Lettuce; and many others

II MONOCOTYLEDONS. Embryo with one cotyledon; stem with closed bundles, "scattered" in cross-section; leaves generally parallel-veined; flowers with parts in threes.

§ 12 Gramineæ.

Distinguishing characters :—Grasses with hollow usually cylindrical stems; leaves alternate in two ranks, with sheathing base, the sides of the sheath not united, and with ligule at the top of the sheath; inflorescence racemose, of spikelets of naked hypogynous flowers; perianth none or of two lodicules; stamens 3, *carpel* 1 *with one basal ovule; fruit a caryopsis.*

This is one of the largest and most cosmopolitan orders of Flowering Plants, the grasses occurring everywhere, and many, in the form of cereal crops or of fodder, being cultivated over enormous areas

Many species are herbaceous, but in the warmer regions of the globe the bamboos, which are simply ordinary grasses magnified, take a very important place, some of them reaching a very considerable height. The method of growth can be very clearly seen in the bamboos. Young shoots appear above the ground during the rains, and grow upwards with extraordinary rapidity, bearing only large scale leaves until they are nearly at their full elongation, when the lateral shoots, which bear the green leaves, appear. Of the small grasses, many are annual

and many perennial, the latter often branching very largely at the base and thus giving rise to a tufted habit. A fair number of grasses possess rhizomes, and yet others have creeping stems, which root at the nodes.

The **stem** has a very characteristic structure, with very clearly marked nodes or joints, which are usually swollen. At these the **leaves** are borne in a two-ranked phyllotaxy, which can be very clearly made out in the bamboos or in almost any of the grasses. The base of the leaf is sheathing, and the **sheath** is split on the side away from the blade, the sides of the slit usually overlapping one another (Fig 86, E). The leaf rarely has a petiole, but has a blade of tender construction, usually long and narrow, but very often, in Indian grasses, almost ovate. At the junction of the blade and the sheath there is a little membranous outgrowth, termed the *ligule*.

A great many grasses, which live in dry situations, have leaves which roll up in dry weather, the upper surface having a series of grooves, with stomata at the bottom; in this way the lower surface, which is thick-walled and has no stomata, is presented to the outer air, and transpiration is checked. When the air again becomes moist, the leaf once more unrolls.

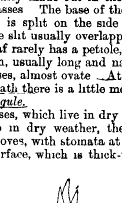


Fig 207.—Typical Spikelet of a Grass

The **inflorescence** is rather complex, and is best considered in terms of the unit of inflorescence, which is not usually a single flower, but a little spike of flowers, known as a *spikelet*. The spikelet may at times possess only one flower. Taking the inflorescence of the ragi, for example, this consists of a group of five or six branches coming off at the top of the stem; along the

outer sides of these branches are the spikelets in a double row. Each **spikelet** (Fig 207) consists of a little stalk along which in the usual two-ranked arrangement are the **glumes** and **inferior paleæ**, or bracts of the flowers. The lowest two of these (the glumes) have usually nothing in their axils, but flowers occur in the axils of the others (the inferior paleæ) The glumes themselves, and to some extent the inferior paleæ also, are boat-shaped with strongly marked keels or midribs. In the axils of the inferior paleæ there stands an exceedingly short axis, on which there is borne first of all a leaf known as the **superior palea,** which is thin and papery, and faces the opposite way to the inferior palea.

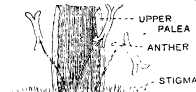


Fig 208 —Typical Flower of a Grass
Lower palea removed

Between the superior and inferior paleæ are the actual essential organs of the flower (Fig 208), consisting of an ovary with two styles, three stamens, and two thin membranous leaves called the **lodicules,** which stand on the same side as the inferior palea. When the flower is about to open, the lodicules expand and push the paleæ apart. They are often looked upon as a rudimentary perianth (Fig 209), but are more probably the representation of a second bracteole (the superior palea being the first), and the flower is consequently completely naked.

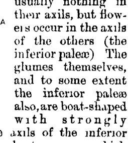


Fig 209 —Floral Diagram of a Grass
(Cf with Fig 145)

The **stamens** are usually three, with long filaments and versatile anthers, whilst the carpel is solitary, forming a 1-locular **ovary,** with two stigmas which are much branched. The ovary being of one carpel only, the two stigmas must be regarded as developments of a single stigma. The **fruit** (Figs 39, 162 c) is called a *caryopsis*, or achene whose seed-coat is completely united to the pericarp At the one end, usually the pointed end of the seed, is the embryo, which is straight, with its only cotyledon, the *scutellum*, wrapping quite round the embryo In germination the cotyledon remains within the seed or embryo, extracting the nourishment from the endosperm, and afterwards becomes withered . Often one or more of the glumes or paleæ runs out into a long thread-like outgrowth, termed an *awn*.

The grasses are **wind-pollinated,** as is indicated by the absence of conspicuous colour and of honey in the flowers, by the easily movable condition of the stamens and their plentiful production of pollen, and by the largeness of the stigmas. The construction of the stamens enables them to shake out their pollen readily, and that of the styles enables them to catch it.

The two chief uses of the grasses are as cereals and fodder The cereals include wheat, barley, oats, rye, maize, ragi, sorghum, the millets, and many others, furnishing the staples of food to mankind throughout the world, while the numerous species used as fodders are of almost equal importance to the animal world, and the bamboos furnish building materials, pots, water channels, and many other articles of daily use to the natives of warm countries.

Of the enormous number of grasses found in tropical Asia, mention can only be made of a few of the most important The chief of these are the cereals, the principal of which are Rice (*Oryza sativa*) in the south and Wheat (*Triticum vulgare*) in the north, though very many others are also cultivated, among which may be mentioned Maize (*Zea Mais*), Italian Millet (*Setaria italica*), Guinea Corn, Juwar, or Great Millet (*Sorghum vulgare*), Ragi or Kurakhan (*Eleusine coracana*), Bulrush Millet, Bajri, or Kumbu (*Pennisetum typhoideum*), and several others. Sugar-cane (*Saccharum officinarum*) is cultivated over enormous areas in India.

Another important group of grasses is the oil-yielding species, such as Citronella (*Cymbopogon Nardus* and *C. Winterianus*), Lemon Grass (*C. flexuosus* and *C. citratus*), Rusa or Geranium-oil (*C. Martini*), Khas-Khas (*Andropogon muricatus*), etc. These all have a strongly scented volatile oil, which is obtained from them by distillation.

§ 13 Palmæ.

Distinguishing characters.—Palms; leaves large, alternate, pinnate or palmate; inflorescence racemose, of hypogynous often unisexual flowers; perianth in two whorls of 3, *stamens ditto; ovary of* 3 *or* (3) *carpels, fruit a berry or drupe, with albuminous seeds.*

This is a large order, confined to the tropics and the subtropics, where they often form very characteristic features in the vegetation, though this is much better shown in tropical America than in Asia, where the palms are most familiar in the vast cultivated belts of coconuts and palmyra palms along the coasts, the former in the damper and warmer regions The vegetative habit of the palms is familiar, and is seen most typically in the Palmyra Palm—a tall straight stem with a crown of leaves, either of fan or of feather shape, at the top. The two most familiar departures from this are the Coconut, which has a stem that rises in a curve (apparently by reason of heliotropic curvature, as it always rises towards the light, and the stems on the outer sides of a clump always bend outwards), and the Toddy Palm, which has its large much branched feather leaves scattered over quite a considerable length of the top of the stem

Many palms, *e.g* the Sago Palm, have rhizomes which creep along below the ground, bending up at the end when about to flower, and others, chiefly the rattans (*Calamus*), have climbing stems, which climb by aid of stout prickles that replace the leaflets at the outer ends of the large leaves. Owing to the fact that the older leaves fall off as the younger come on, the area exposed to the wind does not increase as the palm grows older, and the stem, though it increases in height, does not appreciably increase in thickness after it has once, in its youth, reached its full

diameter On the other hand, the strain at the base increases as it grows taller, and this is met by the formation of numerous adventitious roots which give it a better grip upon the soil

The **leaf** of the palms is very characteristic, and has very few like it outside the family. The leaf, which may be of either pinnate or palmate form, arises by a peculiar process of development, forming in situ as one mass which is split up by a sort of absciss layers The leaf is generally very large, and must therefore have a very good attachment to the stem to prevent its being torn away; this is provided by the formation of a great sheath at the base, which is very often very fibrous, the fibres in many cases, as in the Palmyra Palm, forming valuable sources of commercial coarse fibre The pinnæ are folded where they join the rachis of the leaf, sometimes downwards (reduplicate, or ∧ in section), sometimes upwards (induplicate, or V in section). The surface of the leaf itself is glossy owing to the presence of a thick cuticle, for the palms are in general sun-plants, requiring considerable protection against excessive transpiration; this is also shown in the way the young leaf, unopened, emerges from the bud in a straight vertical line, and does not spread out and expose the comparatively thin blades to the sun till it is nearly mature

The **inflorescence** is large and much branched in most palms In a few palms, such as the Talipot (*Corypha*) and the Sago (*Metroxylon*), it is terminal, and ends the life of the plant The Talipot, for example, grows vegetatively for 40-70 years, and then at last produces a huge terminal inflorescence, which may reach the height of 40 feet, and may contain several million flowers. This, and the vast number of fruits which follow it, are produced at the expense of the enormous quantity of reserves which the palm has been storing up in the stem, and when the fruits are ripe this is exhausted and the palm soon dies. Even in a palm like the Coconut, which flowers all its life, there is a great rush of sap from reserves to the inflorescence, and this is taken advantage of by the drawers of toddy, who tap the young inflorescence to obtain the

sap, which forms toddy, and when fermented yields alcohol, or when evaporated yields sugar.

Sometimes the inflorescences are in the axils of the current leaves, sometimes lower on the stem, in the Toddy Palm, for instance, they appear in descending order along the stem. The branching of the inflorescence is racemose, and it is enclosed in a spathe of one or more

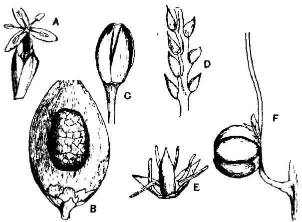


Fig 210 —A, Male Flower of *Borassus* B, Fruit of *Areca Catechu*, half of fibrous fleshy part cut away C, Female Flower of *Areca Catechu* D, Branch of inflorescence of *Areca Catechu*, with male flowers E, Male Flower of *Cocos nucifera* F, Part of spadix of *Cocos nucifera*, with one female flower at the base, and two male flowers behind it (After Drude)

leaves, out of which it bursts when ripe The individual flowers are sometimes free, but very often they are sunk in the tissue of the stalk, and the inflorescence is then termed a *spadix* (p 249) Sometimes the palm is diœcious, sometimes monœcious (Fig. 210, D, F), and in the latter case it often has the flowers in little cymes of three, one female between two males, this may be well seen in the Toddy Palm (*Caryota*)

The **flower** (Fig. 210, A, C, E) itself has usually a perianth in two whorls of three leaves, alike in colour and

texture The stamens are also in two whorls of 3, and the carpels 3 or (3), in the latter case forming a 1- or a 3-locular ovary, with 3, or sometimes 1, usually anatropous ovules. The flowers are sometimes pollinated by wind, sometimes by insects, but as yet little is known about them in this respect.

The **fruit** (Fig. 210, B) is a berry or a drupe with the endocarp united to the seed In the Sago Palm and others of that group of the family it is covered with hard scales. The seed has a large endosperm, which in the case of the date, the vegetable ivory, and others is formed of cellulose, deposited upon the cell walls, and making the seed extremely hard. When the seed germinates, the cotyledon lengthens and pushes out the radicle, and the plumule subsequently grows out of the cotyledon sheath.

The most important palms in India are the cultivated species, of which the chief is perhaps the Coconut (*Cocos nucifera*), though the Palmyra is almost equally important The Coconut is one of the important agricultural crop plants of the world, and is cultivated over large and extending areas in the tropics These are chiefly near to the sea, for it is a maritime plant, and its seeds are floated long distances uninjured in their fibrous husks, so that the real country of origin of this palm is still unsettled, though it has been carried by man or by the waves to almost every tropical coast. The fruit of this palm is one-seeded, the outer layer of the pericarp fibrous, the inner hard and woody; at the base of the latter are three marks which correspond to the three loculi of the ovary, two of which disappear in the course of development of the fruit Inside the fruit when young is a quantity of watery fluid, which makes a refreshing drink, as the endosperm, which forms the "meat" of the coconut, increases, this fluid diminishes and finally the ripe nut is left with little or none of it

The endosperm contains large quantities of oil, and is largely used as a source of it, being usually dried in the sun to form copra, which is then crushed for the extraction of the oil. The leaves of the palm, woven into "cadjans," are used for thatching; the outer wood of the stem is used

for many purposes. The fruit contains a large quantity of fibres, arranged nearly parallel, in the outer layer of the pericarp; these are obtained by rotting away the soft tissue between them in water, and used as a very important source of coarse fibre (coir), being made into ropes, mats, and other articles The inflorescence, as already mentioned, is tapped when young for toddy, which when evaporated yields jaggery or sugar, and when fermented and distilled yields arrack.

In the same way, the Palmyra Palm (*Borassus flabellifer*) is the source of almost everything that can be required to a large population The wood of the stem is used, the leaves are employed for thatching, the fruit is eaten, the fibre at the base of the leaves is collected and used for brushes, the young inflorescence is tapped for toddy, from which are made arrack and jaggery, and so on. An ancient Tamil song in praise of the palm enumerates 801 uses that can be made of it It occupies enormous areas in the drier portions of southern India

Yet another important cultivated palm is the Toddy Palm (*Caryota urens*), which is more specially used for toddy making, whilst the large stem, split in half and hollowed out, is employed as a water channel. The Betel-nut Palm (*Areca Catechu*) is largely cultivated in Bengal and other parts; its nuts are sliced and chewed with the leaves of the Betel-pepper (*Piper Betle*) by a large part of the population of India

The Talipot Palm (*Corypha umbraculifera*) is another characteristic feature in the south, where its gigantic fan-shaped leaves, and its still more gigantic terminal inflorescence, of which we have already spoken, attract attention everywhere The leaves, cut into large pieces, are used as umbrellas, and cut into narrow strips form the old books upon which so many of the sacred writings have been handed down; writing upon them is done with a sharp metal stylus, and charcoal rubbed in, making a permanent and indelible record. In the Malay peninsula, and in Ceylon and the far south of India, the climbing Calamus palms, known as rattans, are of some importance, their stems furnishing the rattan canes of commerce. The

leaves of *Nipa fruticans*, abundant in the Sundarbans and elsewhere on the coast, form the very best cadjans. This and *Phœnix sylvestris*, the Indian Date, are the only wild palms, perhaps, that form any conspicuous feature in the floral landscape of India.

§ 14 **Araceæ** (Aroideæ).

Distinguishing characters:—Herbs, climbing shrubs, etc., with adventitious roots, and flowers usually in a spadix surrounded by a spathe, ☿ or unisexual, with or without a perianth; stamens typically 6, *but generally less, and often united, ovary of* 1 *or more carpels, fruit a berry.*

This is a large family, very well represented in the tropics, and in India most familiar in the Colocasias and Alocasias, everywhere cultivated as "yams" in the warmer parts and in certain creeping plants often cultivated for ornament Some are herbs with tubers or rhizomes, some climbing plants with aerial roots, one (*Pistia*) a water plant The climbers have two types of aerial roots, those of the one type show great negative heliotropism, and cling closely to the support, while those of the other show marked sensitiveness to gravity, grow down to the soil and absorb nutriment there.

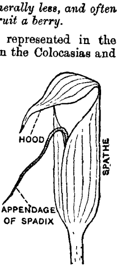


Fig. 211 —Spadix of *Arisæma.*

The **flowers** are usually in spadices (Fig 148), closely crowded together and surrounded by a large spathe, and may be ☿ or unisexual, with or without a perianth, and with typically 6 stamens, usually reduced in number and often united into a *synandrium*. The **fruit** is a berry.

The **rhizomes** or tubers contain much starch, and are very valuable as food. *Colocasia antiquorum*, the Taro, and several species of *Alocasia* and sometimes others, are

used as food in India. *Pistia Stratiotes* is the Water Lettuce, common on ponds, and there are many climbing Aroids also *Arisæma* (Fig. 211) is a large genus, species of which occur all over temperate Himalaya, in the Western Ghats, and in the Nilgiris. *A. Wallichianum* is called the Sánp Bútí (Snake Plant). The plants of this genus are usually either male or female

§ 15. Commelinaceæ.

Distinguishing characters:—Herbs with jointed stems, leaves alternate, sheathing; inflorescence a cincinnus of ☿, regular, usually blue flowers, calyx and corolla 3, stamens 3 + 3, some usually absent or staminodial; ovary superior, of 3 carpels, with axile placentation; fruit a capsule; seeds with endosperm.

This is a little order of tropical and subtropical plants well represented by several common weeds. They are herbaceous plants with jointed stems, and alternate sheathing leaves with narrow, sometimes almost grass-like, blades. The **inflorescence** comes out of a closely folded leaf, and is really a cyme of the type sometimes known as a boragoid, because it is most typically shown in the order Boraginaceæ, to which the Heliotropes and Sebestens belong It is a monochasial cyme in which each successive branch falls alternately on one and upon the other side of what is for the time the main axis, and in the case of the boragoid is much condensed with short axes.

The **flower** is ☿ and regular, or very slightly irregular owing to abortion of some of the stamens, and is usually blue in colour Unlike many monocotyledons, the **calyx** and **corolla** differ in colour, the former being green; each consists typically of three leaves. The **stamens** are typically 6 in two whorls, but very commonly some of them are absent or represented only by staminodes. The **ovary** consists of 3 carpels and has 3 loculi, with a few orthotropous ovules in each. The **fruit** is a loculicidal or indehiscent capsule; the seeds have fleshy endosperm, and sometimes an aril

The order is mainly represented in India by a few com-

mon weeds belonging to the genera *Cyanotis*, *Aneilema*, and *Commelina*. *Commelina benghalensis*, *C. obliqua* and a few other species of the genus occur throughout India The simple, open, very slightly irregular flowers are visited by a large circle of insects.

In the exotic genus *Tradescantia*, which is largely cultivated, all the six stamens are functional. The filaments are covered with long multicellular hairs, the cells of which are a favourable object for observing protoplasmic circulation. (See p 190)

§ 16. **Liliaceæ.**

Distinguishing characters:—Perianth usually petaloid; flowers hypogynous; 6 stamens; trilocular ovary

This is a very large order, comprising about 200 genera The plants are mostly herbs perennating by means of rhizomes, bulbs, *e g* Lily, Onion. and Hyacinth (Fig. 55),

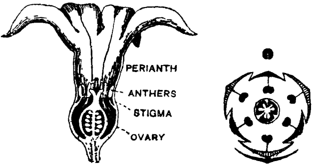


Fig 212 —FLOWER AND FLORAL DIAGRAM OF GARDEN HYACINTH

or corms. A few are shrubs or trees, e g. *Dracæna* and *Yucca*, often showing secondary growth (p 129). Some reproduce by means of bulbils, e g. *Lilium bulbiferum*. Some are climbing plants, e g *Smilax* (p. 147) and *Gloriosa superba* (Kulhárí) *Ruscus*, the Butcher's Broom, and *Asparagus* have phylloclades. Many species are xerophytic.

The **inflorescence** may be racemose or cymose. The umbellate heads found in many, *e.g.* Onion, are cymose. In the Tulip there is a solitary terminal flower. The **flowers** (Figs. 145, 212) are actinomorphic, usually hermaphrodite, typically trimerous and hypogynous. The **perianth** consists of six parts in two whorls, and is usually gamophyllous, occasionally polyphyllous (*e g.* Tulip). There are six **stamens** in two whorls, hypogynous or epiphyllous, with usually introrse anthers. The **pistil** is tricarpellary, syncarpous, the ovary trilocular, superior; the ovules indefinite, anatropous; the placentation axile. The **fruit** is usually a loculicidal or septicidal capsule, occasionally a berry (e g. *Asparagus* and *Smilax*). The **seed** is albuminous.

In many cases the flowers are pendulous (the pollen being thus protected, and cross-pollination promoted), while the capsules are erect, and the seeds blown out gradually by the action of the wind (censer-mechanism)

Pollination.—Both self-pollination and cross-pollination occur, most of the flowers being adapted for long-tongued insects In most cases honey is produced by glandular tissue in the partitions between the chambers of the ovary. In *Lilium* it is secreted at the base of the perianth leaves In Tulip and Garlic there is no honey; the flowers are visited for pollen. In Herb Paris the dusky colour and fetid smell of the flower attract carrion-loving flies.

Some of the more important Indian members of this order are — Various species of the genus *Lilium* (the Lilies) in the Temperate Himalaya, *Smilax*, with stipule-tendrils and net-veined leaves, the roots of some species yielding the drug Sarsaparilla; *Asparagus*, with reduced scale-like leaves bearing in their axils cladodes which appear like tufts of linear leaves; *Gloriosa superba* (Kulhárí), which climbs by means of the tendril-like leaf-tips, *Allium* spp (*A. Cepa*, the Onion or Piáz, *A. sativum*, the Garlic or Lassan, both cultivated, besides many spp wild in the N.-W. Himalaya), *Asphodelus* spp, in the plains and lower hills.

§ 17. Amaryllidaceæ.

Distinguishing characters:—Mostly herbs with inflorescence on a scape, with a spathe; flower regular or not,

perianth 6, *petaloid, sometimes with a corona, epigynous, stamens* 6, *ovary inferior, of* (3) *carpels, trilocular; fruit usually a capsule.*

The most familiar plant of this order in India is the great Agave, of which several species are to be found in a semi-wild condition along railway lines and elsewhere. This species, and in fact the bulk of the order, shows

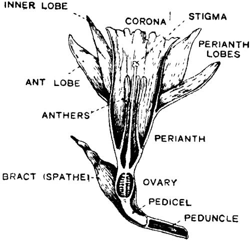


FIG. 213. FLOWER OF DAFFODIL IN VERTICAL SECTION

marked xerophytic characters; in *Agave* the leaves are thick and fleshy, and covered with wax; in others the plant is bulbous, and during the dry season remains in the condition of a leafless bulb. Many species have rhizomes, and give off a leafy shoot each year.

The **inflorescence** is cymose, but very often the flowers arise so closely together that it becomes of head or umbel form, but that it is not a true head or umbel is to be recognised by the fact that the order of the opening of the flowers is not centripetal, but centrifugal or irregular. The inflorescence is generally borne upon a *scape*, spring-

ing from the base of the plant, enclosed at first in a *spathe* of one or more leaves borne on the inflorescence axis

The **flower** is ☿, regular or more or less zygomorphic. It has a petaloid **perianth** of 6 segments; in *Narcissus* and a few others there is within this what is known as the *corona*, a shallow tubular petaloid outgrowth which is sometimes supposed to be the combined stipular outgrowths of the stamens. The **stamens** are 6 with introrse anthers, and below the insertion of the perianth is an inferior **ovary** of (3) carpels, trilocular, with axile placentæ bearing numerous anatropous ovules, and which usually ripens into a capsule, but sometimes into a berry

The commonest members of this family are perhaps the little yellow-flowered Curculigos, but by far the most familiar are the enormous Agaves, or Century Plants, which are often to be seen along railway banks and elsewhere; they owe their English name to the fact that the plant, like the Talipot Palm, saves up reserve materials for many years, and then spends it all in one burst of flowering, in which there appears a gigantic terminal inflorescence, after the ripening of the seeds of which the plant dies A very considerable amount of vegetative reproduction is performed by the aid of little **bulbils**, or small bulbs, which appear in place of many of the flowers of the inflorescence, and sprout when they fall off in suitable places and weather

§ 18 Iridaceæ.

Distinguishing characters:—Perianth petaloid; flowers epigynous; 3 stamens, inferior trilocular ovary

The Iridaceæ are largely represented in dry sunny countries (South Africa, etc) Familiar plants are the Crocus, Iris or Flag, and Freesia. Most of them perennate by means of corms (*Crocus*, p 86, Fig 53), or sympodial rhizomes (many species of *Iris*) The leaves are often equitant and isobilateral (Fig 101), e.g. *Iris*

The **inflorescences** are usually small cymes variously arranged. Thus in the Iris the flowering axis ends in a flower (which opens first), and has small lateral cymes



Fig. 214 —Vertical Section of Flower of Iris (After Church)

On the left are shown an outer perianth segment, a petaloid style entire, and an inner posterior perianth segment cut in half. On the right an outer anterior perianth segment and a style are cut in half showing a stamen lying between them, at the back is a lateral inner perianth segment (petal) s = stigma, bract and bracteoles are also shown.

each invested by a spathe. The **flowers** (Fig 214) are hermaphrodite, regular (*Iris* and *Crocus*), or zygomorphic (*Freesia*), epigynous. **Perianth** of six segments in two series, gamophyllous, petaloid, superior.

Andrœcium of three epiphyllous stamens, they represent the outer whorl, the inner whorl being suppressed, and are situated between the carpels and the outer perianth segments. The anthers are extrorse and lie on the outer side of the styles **Gynæceum** tricarpellary, syncarpous, *ovary* inferior, trilocular, with ∞ anatropous ovules; *placentation* axile The *styles* are united below, but free above, and sometimes expand into three large petaloid lobes (*Iris*). **Fruit** a loculicidal capsule. **Seed** albuminous

Floral formula:—

$$\widehat{P(3+3)}\,A3+0\,G(\overline{3})$$

In the **Crocus** honey is secreted by a nectary on top of the ovary (which is at first underground), and rises

to the mouth of the long slender perianth tube The flowers are protandrous, and are pollinated by bees or butterflies, which touch the stigmas before the anthers. Failing cross pollination, self-pollination may occur. In the **Iris** (see Fig 214) the anthers and pollen are protected by the petaloid styles The stigmas are three thin membranes developed on the outer surfaces of the styles just above the anthers. Honey is secreted by the tissue of the basal portion of the perianth tube. A bee on entering the flower first pushes against the upper surface of the stigma, which alone is receptive, and then brushes the extrorse anthers It is guided in many species by broad bands of hairs (known as the "beard") developed on the perianth segments.

The Indian Iridaceæ are perhaps best seen in Kashmir, where many species of *Iris* occur, both in the wild state and cultivated on the roofs of houses and in grave-yards These, along with the Saffron or Kesar (*Crocus sativus*), which is largely grown in the Valley, form a notable feature of the landscape in some parts of Kashmir.

§ 19 Musaceæ.

Distinguishing characters:—Usually large herbs, with very large oval leaves and cymes or racemes of irregular flowers, perianth 3 + 3 free or united, stamens 3 + 2 and a staminode; ovary inferior of (3) carpels, 3-locular; fruit a berry, capsule, or schizocarp.

Though a small order, this includes the important genus *Musa* (Banana, Plantain). The plants of this genus are gigantic herbs, with what at first looks like a tall stem, but which in reality is the bases of the leaves rolled one over another. The blades of the leaves are large and oval, with a stout midrib, and with parallel lateral veins running from it to the edge of the leaf In windy weather the leaf tears down between these lateral ribs, so that it becomes practically equivalent to a pinnate leaf In *Ravenala*, however, which is not infrequently cultivated for ornament, there is a genuine stem above the ground

The **flowers** are arranged in cymose or racemose inflorescences, with large and brightly-coloured bracts, and are usually ☿. They have a petaloid **perianth** of two whorls of three leaves each, which may be free or united The **stamens** are 5, with a staminode which represents

the missing member of the inner whorl The inferior **ovary** is of 3 carpels, tri-locular, with 1 to many ovules in each loculus, and ripens to a berry (as in the Banana and Plantain), a capsule, or a schizocarp. In the Plantain of cultivation, the seeds are usually absent, except in one variety, in which they are often to be found as hard round bodies in the flesh of the Plantain, but in the rest of the order they occur, with mealy perisperm, or growth of the nucellar tissue of the ovule

Musa is the only important genus of the family, and includes the Banana and Plantain (Kelá). The other genera are *Strelitzia*, *Ravenala*, and *Heliconia*, which are often cultivated *Strelitzia* is pollinated by birds.

§ 20. **Orchidaceæ.**

Distinguishing characters:—Herbs, often epiphytic, with aerial roots and often with pseudobulbs, leaves alternate, simple, inflorescence racemose, often a spike, of irregular, epigynous, ☿ *flowers variously adapted for cross pollination by insects; perianth in two whorls of* 3, *petaloid, very irregular; stamens* 1 *or* 2, *united to the style to form a column; ovary inferior of* (3) *carpels with* ∞ *ovules; fruit a capsule, seeds minute.*

This is the largest order in the flora of India, being represented by about 1,600 species, mostly found in the mountain regions, especially of the Himalaya and Burma. Owing to the diversity of conditions under which they exist they show a great variety in habit and structure, some being land plants, some saprophytes, but the majority epiphytes

The plant may be built up in one of several ways Sometimes it is a **monopodium**, the main axis growing steadily along, and bearing the flowers upon lateral branches, sometimes it is a **sympodium** (Fig 215), made up of successive portions, each of which first appears as a branch upon its predecessor, but takes up the straight line of the axis, while what was previously the main axis goes off to one side or aborts altogether. The sympodium may be *acranthous*, the successive portions each

in turn terminating in an inflorescence, or *pleuranthous*, in which the flowers are borne on side shoots, and the temporarily main axis simply ends off short when it has given rise to the branch which will continue the straight line.

The great bulk of the tropical orchids are epiphytic, living perched upon other plants without being parasitic upon them. The extreme lightness of their seeds fits them to reach such positions with ease, and their xero-

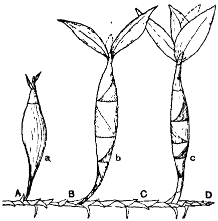


Fig 215 — DIAGRAM OF SYMPODIUM OF AN ORCHID

A, B, C, D, the shoots of successive years, the terminal portions marked *a*, *b*, *c* A, *a* together form one year's growth, similarly with B, *b*, etc

phytic habit fits them to retain possession of them when attained. Most of them are sympodial, but the group also includes the few monopodial orchids Among the most interesting features about this group of orchids are the **roots**, which are of two or more different types. The plant is fastened to the supporting tree by clasping roots, which are not sensitive to gravity, but are negatively heliotropic, and curve away from the light into all the dark corners of the support The latter forms a crevice with the body of the orchid, into which rubbish falls, and

into this the plant sends absorbing roots, which are usually branches from the others, whilst finally there are the true aerial roots which hang down from the plant in festoons, and give it the characteristic appearance which is presented by most of these "air-plants." These roots look whitish on the surface, their appearance being due to the fact that they have a layer of dead, perforated, superficial cells (the *velamen*), which acts as a sponge, soaking up the water which flows over them, whilst their internal tissues are green and perform the work of assimilation.

During the dry season, many or most of the orchids drop their leaves, and rest in the condition of **pseudobulbs**, or fleshy swollen stem tubers, formed of one or more internodes, until the advent of the rains. Very often, however, they flower during this period. As a rule they form one pseudobulb every year, but usually many pseudobulbs may be seen alive side by side upon the same plant.

The land orchids are comparatively few in the tropics, and have as a rule a rhizome of sympodial construction, which bends up at the end into the flowering and leafy shoot of the current year, the underground growth being taken up by a branch. Most of them, perhaps, form pseudobulbs to tide them over the period of leaflessness, but some form root tubers (Fig 74). The saprophytic orchids are few, and have already been described (p. 197).

The **inflorescence** is racemosely constructed, and is perhaps most commonly a spike, which looks like a raceme owing to the fact that the long thin ovaries of the flowers resemble stalks. In some of the epiphytic orchids the spike is often very long, hanging down from the plant

The **flower** (Fig. 216) shows a great departure from the ordinary types to be seen in most natural orders, and is very irregular. The great majority of the family belong to the suborder *Monandræ*, with one stamen, but the Cypripediums, sometimes grown in conservatories, the Apostasias, which are to be found in Nepal, Assam, Ceylon, etc, and a few others belong to the *Diandræ*, with two stamens We shall consider the former first.

The **perianth** is in two whorls, petaloid, and epigynous. Its description is complicated by the fact that in most orchids the flower is turned through an angle of 180°, or **resupinated**, as it is termed, so that the organs which are really anterior in development come to be posterior in the open flower. Remembering this, the actually anterior, but really developmentally posterior, leaf in the perianth of most species, forms a lip or landing place, the **labellum**, which is usually much larger than the rest of the perianth-leaves. In many orchids this resupination does not take place The structure of the labellum is often very complicated, in correspondence with the complicated nature of the mechanisms for pollination of the flower. The other five leaves of the perianth are usually normal coloured leaves, fairly uniform in appearance. Facing the labellum are the essential organs of the flower, united into a structure called the **column**, which may be variously regarded as an outgrowth of the axis, or as a union of the stamens and style.



Fig 216 —FLOWER, COLUMN, AND POLLINIA OF *Ipsea speciosa*

The construction of the column differs in the two suborders In the monandrous forms (Fig 217) the column exhibits an anther at the top, with under it a more or less projecting beak, the **rostellum**, and under this again two stigmas, which are usually more or less completely confluent into one. The single **anther** represents the really anterior one of the outer whorl—assuming for the moment that the flower is derived from one with two whorls of anthers—whilst the remaining five are en-

tirely absent, though in *Orchis*, which is common in Britain, and which is represented in the diagram (Fig. 218, B), the two remaining stamens of the outer whorl are represented by staminodes The two fertile **stigmas** are the posterior pair, and the third is represented by the rostellum. In the Diandræ, on the other hand, there is a simple stigma on the column, composed of all three united, and there are two anthers, which belong to the inner whorl, and no rostellum (Fig. 218, A) There is usually a big staminode, representing the stamen which is fertile in the Monandræ. The **ovary** in almost all the family is unilocular with three parietal placentas, but in *Apostasia* it is trilocular.

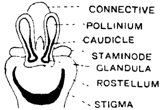


Fig 217 —CENTRAL PART OF FLOWER OF AN ORCHID
Perianth segments removed.

Further complications come in in the internal structure of the anther, where the pollen, instead of being in grains as usual, is united into masses called **pollinia**, which may

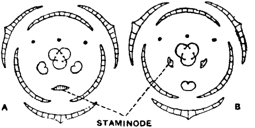


Fig 218 —FLORAL DIAGRAMS OF ORCHIDACEÆ.
A, Cypripedium, B, Orchis

be of any even number from 2 to 8. In these pollinia the pollen grains are tied together by elastic threads, which unite at the base to form a cord, the *caudicle*, which runs down into the rostellum, where it is often united to a

sticky disc or *glandula*, formed of disorganised cells (Fig. 129, c).

We have here described the simpler construction which may be found in a great many orchids, but usually it is more complex than this, very often there are outgrowths of the summit of the receptacle, carrying the labellum and other perianth leaves out to the end of a *chin*, which makes the other leaves of the perianth look as if they sprang from the labellum.

The **fruit** is a capsule, containing a vast number of very minute seeds The ovules do not develop until pollination of the flower has taken place. The seeds are well adapted for wind-dispersal, floating in the air like dust.

No order of plants has aroused so much interest as the orchids with regard to mechanisms for **pollination,** these being of the most extraordinary variety and complication The standard work on this subject, and one which can always be read with great interest, is Darwin's *Fertilisation of Orchids*. As most of the Indian forms have not been examined in this respect, only a few general features can be described The general object, so to speak, being to get the whole pollinium removed and inserted in the stigma of another flower, the various mechanisms are devised so as to secure this end. As the insect enters the flower, it usually depresses the rostellum, and comes into contact with the sticky disc which is therein enclosed, and which when exposed to the air hardens, fastening the pollinia firmly to the insect To allow of this taking place properly, the insect must be detained some time in the flower, and this is secured by there being no free honey, so that the visitor has to bore into the tissue of the spur, or other part of the base of the flower. He then flies away with the pollinia attached to the head, and inserts them into the stigma of the next flower visited, sometimes the pollinia after attachment undergo movements to place them in the suitable position.

The number of orchids in the flora of India is enormous, but they are mostly confined to the hills *Zeuxine sulcata*, however, is ubiquitous in the plains. The Orchids of North-west Himalaya are

remarkable in being mostly terrestrial, while epiphytic species preponderate in the Eastern Himalaya. Many species of *Cœlogyne*, *Vanda*, *Dendrobium* and *Habenaria* are found. Some species of the last-named genus have spurs several inches long *Spiranthes* (the Lady's Tresses), so called because of the spirally twisted flowering shoot, *Neottia* (the Bird's Nest Orchid); *Cypripedium* (the Lady's Slipper Orchid), whose generic name has reference to the shape of the labellum, and *Satyrium*, which has two spurs, are among the most interesting of Himalayan orchids The only orchid of any economic importance is *Vanilla planifolia*, whose pods, carefully collected and dried, form the vanilla of commerce, but there are many of the family which are extremely popular in cultivation on account of their beautiful flowers

PART III—VASCULAR CRYPTOGAMS AND FLOWERING PLANTS

CHAPTER XV

THE VASCULAR CRYPTOGAMS OR PTERIDOPHYTA

§ 1 It is necessary to study several types if we wish to obtain a clear idea of the characters and course of the life history in Vascular Cryptogams and if we wish further to trace the morphological and developmental resemblances i e *homologies* which exist between them and the Flowering Plants The life histories of the Fern Horse tail (*Equisetum*) and *Selaginella* are suitable for this purpose

A LIFE HISTORY OF THE FERN

§ 2 **General Characters**—The Ferns are by far the most important group of the Pteridophyta or Vascular Cryptogams They are for the most part shade and moisture loving plants and grow abundantly in woods hedges and on hill sides A few however are xerophilous and in the tropics there are many epiphytic forms

The fern plant shows a well marked differentiation into root, stem, and leaf The stem has various forms—*e g* in the Tree ferns of the tropics it is aerial, erect, and unbranched but in most cases it is a *rhizome*, growing either horizontally or obliquely upwards through the soil The roots are fibrous and *adventitious* being developed from the surface of the rhizome or from the leaf bases

The leaves are usually large and highly developed The lamina is sometimes entire (e g the Hart s tongue Fern), but is usually much divided

To illustrate the structure and life history of the group we shall consider more especially *Aspidium filix mas* the Male Shield Fern Reference however will also be made to *Pteris aquilina*, the common Bracken Both these Ferns occur in India the Bracken being found practically all over the world

§ 3 **Rhizome, Leaf, and Root** —The rhizome in *Aspidium* (Fig 219) is almost erect, its apex just reaching

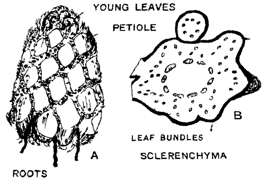


Fig 219 —RHIZOME OF ASPIDIUM
A Upper part from which the older leaves have been cut off at the base and most of the roots removed B diagrammatic transverse section

the surface It is a stout structure, and its surface is covered and concealed by numerous persistent leaf-bases. There is usually no lateral branching, but adventitious buds are developed on the bases of the leaves, and these may separate to form new plants Lateral branching occurs in many ferns, but it is rarely axillary As the rhizome grows in front it gradually decays and dies off behind in this way the adventitious buds or the lateral

branches become separated, and form independent rhizomes.

The leaf is large, compound, and much branched. The dark-coloured base of the petiole is continued upwards as the *rachis*, which bears the green, flattened pinnæ and pinnules. A rosette of leaves unfolds each year, but each leaf takes two years to develop. All the young leaves and the bases of the old leaves are covered with numerous brown ramenta (p 60), which are characteristic of Ferns in general. The *ptyxis* of the leaf is circinate (p 146); this also is characteristic; each leaf is rolled on itself like a crosier from the apex to the base. The venation is described as *furcate* or divergent. One main vein enters each pinnule and gives off branches, which bifurcate and end near the margin without anastomosing

The **fibrous adventitious roots** are developed chiefly from the bases of the leaves.



FIG 220 —PART OF THE VASCULAR SYSTEM OF ASPIDIUM DISSECTED OUT

The dorsiventral rhizome in the **Bracken** is an elongated straggling structure which grows horizontally through the soil and branches at intervals As in *Aspidium*, adventitious buds are developed at the bases of the petioles Only one leaf is unfolded each year on each branch of the rhizome It unfolds in the spring of the third year after beginning its development The leaves are separated by long internodes The rachis is branched In some ferns adventitious buds are developed on the upper surface of the lamina They may separate, strike root, and form new plants

§ 4. **Structure of the Rhizome.**—Fig. 219, B, represents a transverse section of the rhizome. It shows a series of vascular bundles arranged in a ring. The ground-tissue is chiefly parenchymatous, but there is a hypodermal band of sclerenchyma In the ground-tissue outside the ring there is a number of small bundles passing out to the leaves

Fig. 220 shows a portion of the vascular system isolated. The bundles of the ring fuse at intervals and form a cylindrical network surrounding the pith. The meshes of the network correspond to the insertion of the close-set leaves, and are therefore called *leaf gaps*. The bundles passing out to the leaves are given off as branches from the edges of the leaf gaps. There is no secondary growth

§ 5 **Structure of the Bundle.**—The outline of the bundle in transverse section (Fig. 221) is more or less

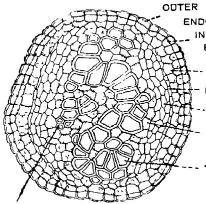


FIG. 221.—BUNDLE OF ASPIDIUM. (Transverse section.)

oval or elliptical In the middle is a mass of wood or **xylem** consisting chiefly of long slender scalariform tracheides (Fig. 222) and small-celled *xylem-parenchyma* containing starch. The bundle, according to its size, may have one, two, or three small **protoxylem** groups These consist of small spiral tracheides. Frequently one is found at each end of the xylem.

The xylem is *surrounded* by the **phloem.** This consists of a layer of sieve-tubes with associated parenchymatous

cells (phloem-parenchyma), and, outside this, a narrow irregular layer of small cells, the **protophloem.** In longitudinal sections the sieve-tubes are seen to consist of narrow elongated pointed cells with albuminous contents. The sieve-tubes contain no starch; numerous *sieve-plates* are present on their lateral walls only; there are *no companion-cells.* These points are characteristic of ferns.

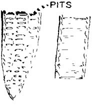


FIG 222 —SCALARIFORM TRACHEIDES OF FERNS

A, B, Small portions of tracheides in surface view

Outside the protophloem is the **pericycle,** which consists of one or two layers of thin-walled starch-containing cells The **endodermis** is single-layered, and its cells lie on the same radii as the cells of the outer pericycle layer, which in origin is probably a sister layer to the endodermis.

§ 6 The Stelar System in Ferns —

The simplest type of vascular structure met with in the stem of Ferns is the **Protostele,** consisting of a solid mass of xylem (or xylem mixed with parenchyma) *completely* surrounded by phloem, pericycle and endodermis in regular order, as shown in Fig 223, A. The vascular supply of the leaf (*leaf-trace*) comes off as a small strand (also consisting of xylem surrounded by phloem, pericycle and endodermis), which may be either rod-like (Fig 223, *a*), or gutter-shaped with the concavity turned towards the stem.

Other Ferns possess a **Solenostele,** which is a tube of xylem lined *both internally and externally* with phloem, pericycle and endodermis, these tissues occurring in the reverse order on the inside (Fig. 223, *b*), so that the internal endodermis immediately surrounds a pith which occupies the centre of the stele The leaf-trace in these solenostelic Ferns usually arises as a single gutter-shaped strand (Fig. 223, B, *b*), which higher up in the leaf may divide up into several pieces. But an important fact is that there is almost always a gap in the xylem tube just in front of an off-coming leaf-trace This gap is called a *leaf-gap* or *foliar gap*, it closes up some distance in front of the leaf-trace At the margin of the gap the internal endodermis, pericycle and phloem meet the corresponding external tissues, and place the central pith into communication with the cortex of the stem. Hence if we dissect out only the xylem portion of such a stem we would obtain a hollow cylinder which is perforated by an elongated gap wherever a leaf arises A trans-

verse section of such a cylinder would therefore be either **C**-shaped or **O**-shaped according as it does or does not pass through a leaf-gap

In solenostelic Ferns the leaves usually do not arise at short intervals, so that the leaf-gaps do not overlap. No single **transverse section**

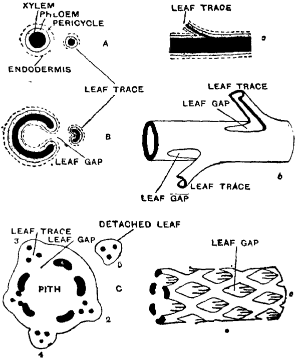


Fig 223 —Diagrams to illustrate types of Vascular System in Ferns.
A, a, Protostele, B, b, Solenostele, C, c, Dictyostele

will pass through more than one gap, on the other hand many of the sections will be gap-less (**O**-shaped). **If, however, we imagine** the leaves to be crowded together on the stem, each leaf producing a gap in the vascular cylinder, we obtain **a Dictyostele,** so called

because of the net-like character of the cylinder (Fig 223, *c*; and Figs 219, 220). The leaf-trace is usually compound, that is, it consists of several small strands These are as a rule clearly arranged in an arc, and are together equivalent to the undivided C-shaped trace of the solenostelic Ferns In a dictyostele the leaf-gaps are so crowded that it is impossible to avoid cutting several (at least two) of them in the same transverse section, hence such a section shows the cylinder broken up into a ring of smaller strands (*meristeles*), each resembling a miniature protostele

Of the three main types of vascular system above described, the protostele is generally met with in the more primitive Ferns (*Hymenophyllum, Trichomanes, Gleichenia* spp , *Lygodium*), the dictyostele in the Higher Ferns (many Polypodiaceæ, such as *Aspidium*), while a large number of Ferns of an intermediate grade of evolution are solenostelic (*Adiantum pedatum*, a common Himalayan Fern, among others)

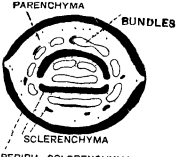


Fig 224 —RHIZOME OF PTERIS.
(Diagrammatic transverse section.)

There are also many Ferns (e g *Pteris aquilina* and Tree-Ferns) which do not quite agree with any of these three types, but these variations need not be described

Hitherto we have considered the stelar system of only the fully developed stems But if we trace the development of a dictyostelic Fern-stem from its earliest stage to the adult condition, we generally find that the young sporophyte has a protostele This protostele, as we trace it forwards into the later-formed parts of the stem, becomes hollowed into a solenostele, and finally, in the mature stem, there is a dictyostele Thus in a dictyostelic Fern a series of transverse sections from the base of the stem upwards will show, in turn,

a transitory protostele, a transitory solenostele, and a permanent dictyostele This discovery is one of the strongest botanical evidences in favour of the **Recapitulation Theory,** according to which an organism during its individual life-time more or less closely repeats its evolutionary history.

§ 7 In the **Bracken Fern** (Figs. 224, 225) there are two series of bundles, between which lie two stout bands of sclerenchyma. The outer bundles are more numerous, but smaller The hypodermal sclerenchyma does not form a continuous band, it is interrupted on each side of the rhizome, and at these points the parenchymatous ground-tissue reaches the epidermis It is in this way that provision is made for the transference of oxygen to the more deeply situated tissues A regular cylindrical network of bundles is usually not found in ferns with dorsiventral rhizomes (Bracken, etc) The leaves are few in number, and the foliar gaps are very much elongated Thus the bundles form long, irregular strands, which fuse only at considerable intervals

§ 8 **Structure and Development of the Root.**—The root contains a number of xylem and phloem strands

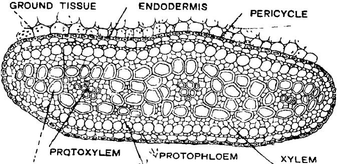


Fig 225:—Bundle of the Rhizome of Pteris. (Transverse section.)

situated on alternate radii In *Aspidium* and most other Ferns the stele is *diarch* (see p 124). The pericycle and endodermis are single layers of thin-walled cells In

the older parts of the root the cortical tissue immediately outside the endodermis is usually strongly lignified, and forms a stout strengthening sheath. The outer cortical tissue is parenchymatous. The outermost layer is the piliferous layer, or epiblema. There is no secondary growth

Lateral branch-roots, while they are *endogenous* in origin, are not developed, as in Flowering Plants, from the pericycle, but from the endodermis. They arise opposite the protoxylem. These root-producing cells of the endodermis are called **rhizogenic cells.** In the same way the adventitious roots developed from the rhizome or petiole take their origin in rhizogenic cells of the endodermis investing a bundle.

§ 9. **Apex of Rhizome and Root** (Fig 226) —At the apex of the rhizome there is, as in Flowering Plants, a mass of meristematic tissue. An important difference,

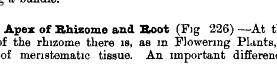


FIG 226 —APEX OF RHIZOME AND ROOT OF FERN
A, Rhizome, B, Root (Diagrammatic longitudinal sections)

however, must be noticed In the Fern there is at the extreme apex one very large distinct cell from which all the tissues are produced. This is the **apical cell.** There is no such single cell in Flowering Plants.

In the rhizomes of most ferns (e g. *Aspidium*) this cell is bounded by four walls—three flat walls meeting in a point below, and a curved wall closing in the cell on top. The cell, therefore, is tetrahedral in form, its apex being directed inwards. Segments are cut off, *in succession*, parallel to the flat walls. After the formation of each segment, the apical cell increases to its original size. The segments are indicated in the figure. There are no segments cut off parallel to the curved wall in the rhizome.

In ferns with distinctly dorsiventral rhizomes (*e g* Bracken) there is a two-sided instead of a three-sided apical cell, and there are, therefore, only two instead of three series of segments.

The segments cut off undergo division, and thus the tissues of the rhizome are produced. The first division is into inner and outer halves (Fig. 226, A). The tissue formed by division of the outer halves corresponds to periblem and gives rise to the cortical ground tissue. All the vascular strands make their appearance in the tissue which is formed from the inner halves, and which corresponds to plerome. The layer of ground-tissue immediately surrounding each vascular strand forms an endodermis. It is evident that there is no distinct dermatogen layer, the outermost layer of tissue is specialised to form the protective external covering, the "epidermis" of the rhizome.

In the **root**, also, there is a single apical cell. It lies just behind the root-cap. In all cases it is three-sided. The segments cut off parallel to the flat walls divide in the same way as in the rhizome; here also the inner halves of the segments constitute the plerome, from which the vascular cylinder is developed. The outer halves may be called the periblem. Segments are also cut off parallel to the curved wall, and give rise to the tissue of the root-cap. These segments represent the **dermatogen**, and the root-cap is as usual to be regarded as a many-layered epidermis. The tissue of the root-cap does not persist behind the apex—hence, the piliferous layer is the outermost layer of cortical tissue. The endodermis represents the innermost layer of cortical tissue.

§ 10. **Structure and Development of the Leaf.**—The leaf is developed exogenously from a single superficial cell of the growing point. This cell persists at the apex of the leaf as a two-sided apical cell until an adult condition is reached. A number of vascular strands enter the petiole from the rhizome (Figs. 219 B, 220). These branch out into the pinnae, where they maintain their concentric structure; but in the pinnules they break up into bundles which are more or less collateral. As is usual in shade-loving plants the palisade and spongy layers of mesophyll are not very sharply differentiated, and the ordinary epidermal cells have chloroplasts. Stomata are confined to the lower surface of the leaf.

§ 11. **Sporangia and Spores.**—Early in the summer a number of structures called **sori** appear on the under surface of the pinnules of the leaves. These are at first of a light green colour, but when older they become dark brown (Fig 227). They are developed immediately over the veins.



Fig 227 —Pinnule of Aspidium bearing Sori

The indusium has been removed from one placenta, the indusium and sporangia from another.

If a young sorus be carefully removed and examined with a lens, it will be found to consist of a collection of very small stalked bodies called **sporangia** which are covered over and protected by a horse-shoe-shaped scale called the **indusium.** The sporangia and indusium are both developed on a little cushion of tissue, the **placenta,** formed immediately over a vein. The relative position of these various parts is clearly shown in Fig. 228, which represents a transverse section of a pinnule passing through a sorus. In some ferns in which the sori are arranged as in *Aspidium* there is no indusium. A sorus, therefore, may be described as a collection of sporangia developed on a placenta, either with or without an indusium.

The fully formed sporangium (Fig 229) is a small structure consisting of a tiny capsule borne on a slender

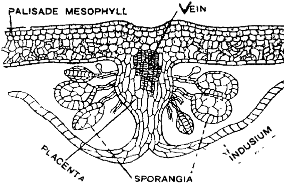


FIG. 228 —SPORANGIA OF ASPIDIUM
(Transverse section through a pinnule and sorus.)

multicellular stalk. The stalk in *Aspidium* often bears a little glandular cell (Fig 228), the function of which is doubtful. The capsule is biconvex, and its wall consists of a single layer of cells The cells are small and thin-walled except round the edge of the capsule, where they are large, specially thickened, and cutinised. This specialised layer, which, however, is incomplete on one side, is called the **annulus**.

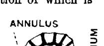


Fig 229 —SPORANGIUM AND SPORE OF FERN.

Inside the capsule lies a loose powdery substance which on examination is found to consist of extremely small reproductive bodies called **spores**. Typically sixty-four of these are produced inside each capsule; but there are usually only forty-eight in *Aspidium*. A sporangium, therefore, is a reproductive organ containing spores. The spore, which is of a brown colour and irregular or somewhat triangular in shape (Fig 229), is a single cell

consisting of protoplasm and nucleus invested by a wall which is differentiated into two layers or coats The inner layer, called the *endosporium*, is thin, and consists of cellulose; the outer, called the *exosporium*, is thickened and cutinised.

Pteris (Fig. 230).—The sporangia and spores have the same structure and appearance as in *Aspidium*, except that no glandular cell is developed on the stalk of the sporangium. The sporangia, however, are differently arranged. Instead of being grouped together in small sori, they are developed in a continuous series on a placenta running along the under margin of the pinnule In other words, there is a continuous **linear sorus.** On the inner side of the placenta in the common Bracken (not in all species of *Pteris*) there is a delicate membrane of a yellow colour, representing a true membranous indusium The margin of the pinnule also, by bending over, serves to protect the sporangia, and is termed a *false indusium*. Between the sporangia are epidermal outgrowths (hairs) called *paraphyses*

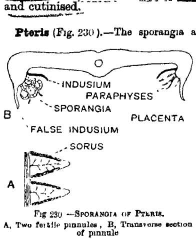


Fig 230 —SPORANGIA OF PTERIS.
A, Two fertile pinnules, B, Transverse section of pinnule

§ 12. **Development of the Sporangium** (Fig. 231) — The sporangium is developed from a single epidermal cell of the placenta. The cell in question grows out and forms a little protuberance, which is cut off by a wall. It is then divided transversely into two cells (A). The lower cell, by further longitudinal and transverse divisions, develops into the stalk.

The upper cell produces the capsule. First of all (B) a series of outer cells is divided off from a large central tetrahedral cell by four walls resembling those bounding the apical cell of the rhizome, *i e.* three flat and one curved (only two of the flat walls can be shown in the figure).

The outer cells, by further divisions at right angles to the surface, form the single-layered wall of the sporangium.

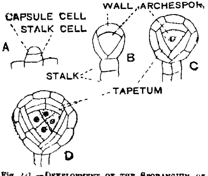


Fig 231.—Development of the Sporangium of the Fern.

The tetrahedral cell is called the **archesporium**. It undergoes division by walls formed parallel to the first set (c). The outer cells so cut off undergo further division, and are called **tapetal cells.** The remaining central cell is the *archesporium proper*; by repeated cell-division it produces, typically, sixteen **spore-mother-cells** (D). These separate from each other, and, owing to the disorganisation of the tapetal cells, float freely in a fluid filling the cavity enclosed by the sporangium wall

The nucleus of each mother-cell divides karyokinetically into two, and these two divide again, so that four nuclei are formed Then cell-walls are laid down between the nuclei, and thus the mother-cell is divided into four cells, called the "*special mother-cells*," in each of which a spore is formed by rejuvenescence (p 45) The protoplasmic contents of each special mother-cell form a cell-wall which is differentiated into exosporium and endosporium. The walls of the special mother-cells are disorganised and the spores lie free in the cavity of the sporangium. The developing spores are partly nourished by the fluid formed by the breaking down of the tapetal cells, and food-materials are conveyed to them through the stalk of the sporangium.

During development some of the cells of the wall of the sporangium are specialised to form the annulus. The archesporium may be defined as the meristematic cell or

cells (single cell in the Fern) which are found in a developing sporangium and give rise to the spores.

§ 13. **The Sporophyll.**—A leaf bearing sporangia is called a sporophyll. In most ferns the sporophylls more or less resemble the ordinary foliage leaves (*Aspidium* and *Pteris*). They are simply leaves which function both as vegetative and reproductive organs. In some ferns, however, the sporophylls differ considerably from the foliage leaves (e g *Osmunda regalis*, the Royal Fern); but there is never a specialised reproductive *shoot* distinct from the ordinary vegetative one (see p. 8)

§ 14. **Germination of the Spore** (Fig. 202).—When the sporangium is ripe, the cells of the annulus become

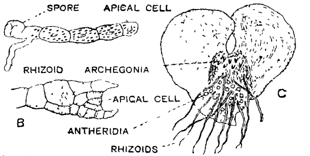


Fig 232.—Germination of Spore and Development of Prothallus of Fern.

dry, contract, and thus put a strain on the thin part of the edge of the capsule. The latter bursts open at this point, the *stomium* (Fig 229), and the spores are set free.

If a spore falls in a suitable soil, it germinates. For germination a supply of oxygen and sufficient warmth and moisture are required. When these conditions are fulfilled the exosporium is ruptured, and the endosporium grows out into a short tube. From this a colourless hair (**rhizoid**) arises, and passes down into the soil. The tube (germ-tube) elongates, and forms at first a short filament

divided into cells by a series of parallel transverse divisions (Fig 232, A). After that, divisions are formed in the other two planes, and a small green flat plate of tissue is produced. This, in early stages, grows by means of a two-sided apical cell (B), but later by a group of meristematic cells. Owing to the more rapid growth of the marginal cells the plate eventually becomes more or less heart-shaped The structure thus developed is called the **prothallus** or *prothallium* (C)

§ 15. **The prothallus** is a very small flat plate of tissue, measuring only one-fourth or one-third of an inch across It consists of rounded parenchymatous cells, containing numerous chloroplasts. Towards the margin it consists of a single layer, but in the central region it is thickened, owing to the division of its cells parallel to the surface This thickened region is called the *cushion* Long, brown, unicellular **rhizoids**, resembling root-hairs, are developed from the cells of the under surface, and pass down into the soil.

It will be recognised that the prothallus is an *independent plant*. By means of its chlorophyll it can assimilate the carbon dioxide of the atmosphere, and by the aid of its rhizoids it absorbs nutritive salts from the soil. It is a distinct self-sustaining plant, whose vegetative body is a thallus (p 7) Owing to its thinness gases can penetrate to all parts with relative ease, and hence no stomata are developed upon it.

§ 16. **The Sexual Reproductive Organs** (Fig 232, C) are produced on the *under* surface of the prothallus—the **antheridia**, or *male sexual organs*, on the posterior region, the **archegonia**, or *female sexual organs*, on the cushion in the anterior region near the notch of the heart-shaped prothallus. The antheridia are developed first.

The *antheridium* (Fig. 233, C) is a spherical capsule, the wall of which consists of a single layer of cells containing chloroplasts * Inside are a number of small cells called

* In some forms the antheridium has a short unicellular stalk.

spermatocytes, or *spermatozoid mother-cells,* each of which gives rise to a male sexual cell, or gamete, the **spermatozoid** (or *antherozoid*).

The *archegonium* (Fig 234, E) is a flask-shaped organ, consisting of two parts (*a*) a swollen basal portion, the *venter*, completely sunk in the tissue of the prothallus, (*b*) a more slender portion called the *neck*, projecting freely from the surface. The venter contains a single large **ovum,** or egg-cell The neck consists of four longitudinal rows of cells surrounding a central canal, which is at first closed at the apex, and which leads down into the venter The neck is not straight, but bends so as to face towards the antheridia. The central canal is filled by two cells, a small **ventral canal cell** lying just above the ovum and a long **neck canal cell** filling the rest of the canal

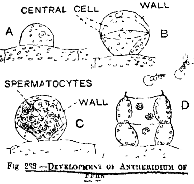


Fig 233 —DEVELOPMENT OF ANTHERIDIUM OF FERN

§ 17. **Development.**—The *antheridium* (Fig 233) is developed from a single cell of the prothallus. The cell grows out to form a papilla-like outgrowth, which is cut off by a cell-wall It increases in size, and two ring-shaped cells and a lid-cell, forming the wall, are marked off from a central cell in which the spermatocytes are formed.

The *archegonium* also is developed from a single cell (Fig. 234, A-F) This cell divides into three The basal cell (B) forms a portion of the tissue surrounding the base of the archegonium. The outermost cell (B) is divided

by two walls at right angles (only one can be shown in the figure) into four cells. These undergo further transverse divisions to form the four longitudinal rows of the neck (C-F). The protoplasm of the central cell (B) pushes its

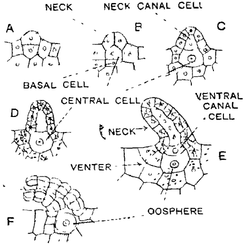


Fig 231 —DEVELOPMENT OF ARCHEGONIUM OF FERN

way between the neck-cells, and a small portion is cut off as the neck-canal-cell (C). The remainder of the protoplasm of the *central cell* undergoes division to form the oosphere and the ventral canal-cell (E). The cavity of the venter of the archegonium is partly lined by prothallus cells.

§ 18 **Fertilisation** (see p 45)—When mature, the antheridium bursts open at the apex owing to absorption of water by the two ring-shaped cells forming the wall and the consequent pressure exerted by them on the contents of the antheridium (Fig 233, D) The spermatozoid mother-cells are thus set free and the spermatozoids escape from them.

Each spermatozoid is a spirally coiled body bearing towards its slender anterior end a number of fine protoplasmic *vibratile* threads called **cilia.** The greater part of the spermatozoid is formed from the *nucleus* of the mother-cell (spermatocyte), but the protoplasm of the mother-cell forms the ciliated region together with a little vesicle, containing starch grains, which remains for some time attached to the posterior end of the spermatozoid.

The spermatozoids move about in the water by means of their cilia. Sooner or later they come into the neighbourhood of archegonia When an archegonium is ripe the two canal-cells are disorganised and give rise to a mucilaginous substance which oozes out of the neck of the archegonium (Fig. 234, F). This substance contains malic acid, which attracts the spermatozoids (chemotaxis—see p. 213) They cluster round the neck of the archegonium, and, finally, one enters the canal and passes down to the venter It penetrates the oosphere and its nucleus fuses with that of the oosphere (cf. Angiosperm, p 267) The fertilised oosphere forms a cell-wall and is then called the *oospore*

Although the prothallus bears as a rule both kinds of sexual organs, and is therefore hermaphrodite (p. 222), cross-fertilisation generally takes place, the spermatozoids developed on one prothallus passing to the archegonia of another. This is necessary because antheridia and archegonia are not developed simultaneously on a prothallus (cf dichogamy, p. 259). Sometimes, in badly nourished prothalli, only antheridia are developed

§ 19 **Development of the Young Fern-Plant** (Figs 235, 236) —The oospore begins to divide or segment, and this process of segmentation leads finally to the development of an embryo The first division-wall is nearly parallel to the long axis of the archegonium. It is called the **basal wall,** and divides the oospore into anterior or **epibasal** and posterior or **hypobasal** halves. A second wall, the transverse or quadrant wall, at right angles to the basal wall, divides the oospore into upper (superior) and lower (inferior) halves. The oospore now consists of four cells (quadrants). Then a median or octant wall at right

angles to the first two divisions divides the oospore into right and left halves. The oospore now consists of eight cells or **octants** (Fig 235).

Of the two superior anterior octants one becomes the apical initial cell of the **primary stem**, the other takes no special part in the development. The two inferior anterior octants give rise to the first leaf or **cotyledon.** Of the two inferior hypobasal octants, one becomes the apical cell of the **primary root**: it is diagonally opposite the cell which produces the primary stem. The two superior hypobasal octants give rise to an embryonic organ called the **foot.** This is a massive structure which absorbs nourishment from the prothallus for the developing embryo, till the latter can assimilate food-material for itself.

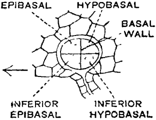


Fig 235.—Segmentation of the Oospore of Fern
The arrow points anteriorly. (Diagrammatic)

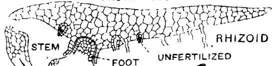


Fig 236 —Embryo of Fern attached to Prothallus.
(Longitudinal section.)

Further cell-division, of course, takes place in the octants marking out the plerome of root and stem The primary stem and cotyledon break forth from the under surface of the prothallus, then bend upwards, make their way through the notch of the prothallus and come above

ground, where they become green.* New leaves are developed, and gradually the stem becomes the rhizome of the fern-plant The primary root is not persistent. At a very early period its place is taken by adventitious roots developed from the stem and leaf-bases (cf. Monocotyledons)

As a rule only one embryo is formed on a prothallus, which then dies In some ferns, however, the prothallus has a longer life, and may reproduce itself vegetatively by means of branches, or little outgrowths of meristematic tissue called gemmæ.

§ 20 **Sporophyte and Gametophyte.—Alternation of Generations.**—It will be noticed that in the life-history of the Fern there are really two plants to be considered These are spoken of as the two *stages* or *generations* of the life-cycle. There is first the fern-plant, so called because it is by far the more conspicuous of the two It is spoken of as the **sporophyte** or asexual generation, because it is the generation which bears the asexual reproductive organs, sporangia and spores Then there is the prothallus, which is called the **gametophyte** or sexual generation, because it is the generation which bears the sexual reproductive organs and the sexual cells or *gametes* (the ovum and spermatozoid)

Now it will be seen that a young sporophyte is *not derived directly* by a sexual process from the parent sporophyte, for a gametophyte generation is interposed between them In the life-cycle there is an alternation of sporophyte and gametophyte. This is spoken of as the **alternation of generations.** The student must observe this phenomenon very carefully, as it is exhibited by all the higher plants (Mosses, Vascular Cryptogams, and Phanerogams) in some form or other. We have explained it in connection with the Fern because it is most clearly exhibited in the group of the Vascular Cryptogams, but it will be shown later (Chapter XV) that it is present also in a modified form in Flowering Plants.

* The cotyledons of many ferns are able to turn green in darkness

§ 21. **Number of Chromosomes.**—It has been found in various plants examined that the number of chromosomes in the nuclei of the cells of the sporophyte is double the number found in those of the gametophyte The doubling of the chromosomes takes place at the time of fertilisation; the reduction to the number characteristic of the gametophyte is effected at the division of the spore mother-cells (see p. 41) This constitutes an important cytological distinction between the two stages in the life-cycle

§ 22. **The Reproductive Processes.** — It will be noticed that both sporophyte and gametophyte begin their development from a single cell, the young sporophyte from an oospore formed as the result of a sexual process (fusion of gametes), the gametophyte from a spore formed

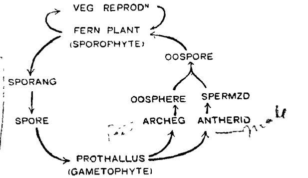


Fig 237 —LIFE HISTORY OF FERN GRAPHICALLY REPRESENTED

asexually This is characteristic of sporophyte and gametophyte wherever there is alternation of generations, the reproductive bodies formed in the one generation giving rise to the other. In the life-cycle of the Fern, then, there is an alternation of generations, and asexual spore-reproduction forms an integral part of it.

Vegetative reproduction is very clearly distinguished It has no share in the alternation of generations, and simply lengthens the life-cycle, either at the sporophyte

stage or at the gametophyte stage, *i e* either generation may directly and indefinitely reproduce itself by vegetative methods, without the intervention of the other generation These points may be illustrated and the general life-history shown graphically in the form of a diagram (Fig. 237).

§ 23. **Apogamy and Apospory.**—While the reproduction of sporophyte and gametophyte is usually effected as above described, there are in some ferns exceptional cases where either (*a*) the spore stage, or (*b*) the sexual process is, as it were, cut out of the life-cycle The former condition is called *apospory*, the latter *apogamy* (see p 271)

Various grades of apospory exist (1) the formation of spores may be suppressed and the prothalli may develop directly from the young sporangia, (2) prothalli may develop from the placentas in the place of sporangia, (3) they may develop vegetatively from any portion of the frond, without any indications of the formation of sori, sporangia or spores

In apogamy the young sporophyte may arise directly as a bud from the tissue of the prothallus without the intervention of sexual organs. This is vegetative apogamy. Or it may be developed from the *unfertilised* oosphere This is *parthenogenesis* or parthenogenetic apogamy (see p 271) It will be noticed that these conditions tend to shorten the life-cycle, and to replace ordinary spore-reproduction or sexual reproduction by a kind of vegetative reproduction

It has also been found that the prothalli of a few cultivated ferns may actually produce normal sporangia containing fertile spores, and thus reproduce themselves by asexual means The spores on germination produce the usual prothalli, which may ultimately give rise to a sexually produced fern plant By such means as these the asexual generation may be suppressed for one or more life-cycles, which latter may subsequently resume their normal succession

B Equisetum

§ 24. **General Structure.**—*Equisetum* is the only remaining genus of a large group of plants which were well represented in earlier periods of the earth's history. Fossil remains of the group have been discovered in many parts of the world, including India, and reveal the fact that some of the ancestors of the present-day Equisetums were large forest trees having secondary growth in the stem.

The plant which we call the Horse-tail is the *sporophyte.*

It consists of a branching horizontal rhizome giving off *aerial* shoots and numerous adventitious roots. The leaves borne on the aerial shoots are small and scaly, most of the photosynthesis being performed by the cortex. They are arranged in whorls, and in each whorl are fused together to form a sheath, which invests the base of the internode above. Whorls of axillary branches may be produced at the nodes.

The stem has longitudinal ridges and grooves which give a wavy appearance to the transverse section. A great

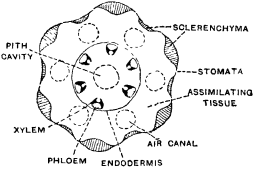


Fig. 238 —*Equisetum*. DIAGRAMMATIC TRANSVERSE SECTION OF STEM

deal of silica is deposited in the outer walls of the epidermal cells, and the stomata, which lie in two parallel rows in each groove, are sunk below the surface, as in *Pinus*. Further protection and strength are afforded by strands of sclerenchyma, specially developed at the ridges. Below each groove the cortex is hollowed into an air-canal with which the stomata communicate by means of small intercellular spaces in the cortex. The assimilating cells lie between and on the outer sides of these canals, where they have easy access to the air.

The cortex is limited on the inner side by a definite endodermis. The vascular bundles are collateral and lie in a ring, one under each ridge of the stem. There is a

thin-walled parenchymatous pith which, however, is hollow in the middle. At each node there is a plate of cells, the *diaphragm*, which separates the pith-cavities of the internodes

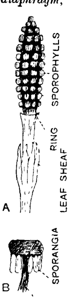


Fig 239 — EQUISETUM
A, Apex of fertile shoot, B, A Sporophyll

The **sporophylls** are produced at the apices of the aerial shoots. They are free and have the form of *stalked peltate discs* (Fig. 239), which are closely packed together in whorls, so that a cone-like mass is formed at the apex of the shoot The lowest whorl is sterile and forms a collar-like structure known as the ring (Fig. 239) This specialisation and aggregation of sporophylls should be carefully noticed. The reproductive region of the shoot is quite distinct from the vegetative portion (see p. 8).

Each sporophyll has on its under surface a group of **sporangia** containing **spores.** The sporangium as a whole is developed from *a group of cells*, although all the essential parts are derived from a single superficial cell After the wall of the sporangium and the tapetal layers have been formed a single large **archesporial cell** remains, which divides to form spores The sporangium has no annulus, but the single-layered wall has its cells spirally thickened Dehiscence occurs by a longitudinal slit facing the stalk of the sporophyll The outer wall of each spore is produced into four hygroscopic bands (*elaters*), which in the wet condition are spirally coiled round the spore, but on drying straighten out and help in the dehiscence of the sporangium

The sporangiferous "spikes," as the conelike structures of *Equisetum* are called, are borne either at the apices of ordinary vegetative shoots, or, in some species, on special fertile or reproductive shoots which resemble the others except that they are unbranched and contain little or no chlorophyll.

§ 25 **General Life-history.**—The spores are all of one kind, *Equisetum*, like most Ferns, being *homosporous* When the spores fall to the ground and germinate, however, they usually give rise to **prothalli** *of two kinds* Some of the spores produce prothalli bearing antheridia only, others produce prothalli bearing archegonia only. The student will remember we have an indication of the same thing occasionally in the Fern (p 404) It has become the rule in *Equisetum*. The differentiation of sex

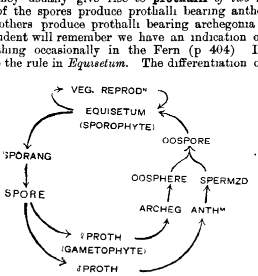


Fig 240 — LIFE HISTORY OF EQUISETUM GRAPHICALLY REPRESENTED

has, as it were, been carried back from the sexual organs (antheridia and archegonia) to the structures bearing these sexual organs, so that we may now speak of male and female prothalli

The prothalli are unisexual, and the gametophyte is represented by two plants They are more or less lobed structures, and *as a rule the male prothalli are much smaller than the female ones* In other characters they resemble those of the Fern, as do also the sexual organs. Fertilisation is effected and an embryo sporophyte developed in much the same way The life-history may be graphically represented as in Fig. 240.

C. SELAGINELLA.

§ 26. **General Characters** (Fig 241) —The plant is the sporophyte. The external vegetative characters vary considerably in the different species, which number about four hundred, and of which a large number occur in the hills in India Many species are small, moss-like plants, with creeping stem and dorsiventral symmetry. Others are larger, and more or less erect and isobilateral. Some species are climbing plants, often growing to a great height

The slender **stem** usually bears four rows of leaves—two rows of small dorsal leaves on the upper surface, two of larger ventral leaves at the sides of the stem. The arrangement of the leaves seems to be opposite and decussate, one large and one small leaf apparently arising at each node The leaves, however, are somewhat twisted, and close examination shows that each leaf arises from its own node, the dorsal leaf being slightly above the opposite ventral one In *Selaginella spinosa* all the leaves are of the same size and the spiral arrangement is immediately obvious In all the species a small membranous **ligule** is developed on the upper surface of the leaf at its base.

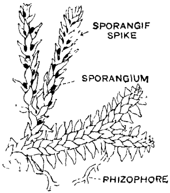


Fig 241 SELAGINELLA HELVETICA

The **branches** are developed from lateral buds which become visible near to the apex of the stem, but since they develop almost as rapidly and as strongly as it does, the branching assumes a dichotomous appearance. The branching is *not axillary*, and the branches all lie in one plane.

The **roots** in some species are developed adventitiously on the stem; in other species they are borne on peculiar specialised branches. called **rhizophores.** These organs

are intermediate in structure and development between roots and stems. Like stems, they have no root-cap, and are developed exogenously; they resemble true roots in internal structure and in the fact that they bear no leaves or reproductive organs. We may infer, however, that they are specialised stem-branches from the fact that *occasionally* they are found to develop into ordinary shoots.

The rhizophores, when present, are given off from the lower surface of the stem, one from below each point where an ordinary branch arises. They grow down to the surface of the soil without branching, but on reaching the soil give rise, by endogenous development, to a number of true roots.

The **reproductive organs** (Figs 241, 243) are produced at certain periods towards the apices of fertile or reproductive shoots These reproductive shoots are more or less *erect*, and, in nearly all the species, bear spirally arranged sporophylls, which do not differ very markedly from the ordinary foliage leaves

The reproductive organs are **sporangia** and **spores.** *One* sporangium is developed *in the axil* of each leaf of the reproductive shoot. The sporangia are of two kinds, **megasporangia** and **microsporangia,** each of the former containing usually four large **megaspores,** each of the latter a large number of small **microspores.** Thus *Selaginella* is *heterosporous* The same sporangiferous "spike" usually bears both kinds, the microsporangia in the axils of the upper leaves, the megasporangia in the axils of the lower, although this is not always the case, for the megasporangia may occur in the middle of the spike

Recently vegetative reproduction (by means of aerial or underground tuber-like structures) has been discovered in two Indian species, *S chrysocaulos* and *S. chrysorrhizos*, from the North-West Himalaya.

§ 27 **Stem** (Fig 242).—In some species there is a single apical cell as in the Fern; in others, a group of two or three initial cells which by their divisions give rise to the tissue of the stem This may be regarded as an intermediate condition between the single apical cell of the Fern and the small-celled meristem, showing dermatogen,

periblem, and plerome, which is characteristic of Flowering Plants

In some species the stem has a single vascular bundle, but most species have two or more bundles. Each bundle is suspended in the middle of a large air-space by a num-

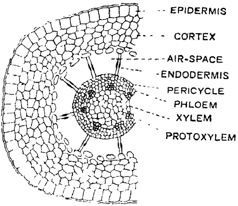


FIG 242.—STEM OF SELAGINELLA SPINOSA.
(Transverse section)

ber of delicate trabeculæ, which represent the stretched endodermis. These often have silica deposited upon them in the form of irregular plates, or annular deposits (Fig 242). The bundle is concentric. The central wood, or **xylem,** consists of slender scalariform tracheides According to the species one, two, or a number of **protoxylem** groups can be distinguished

In *S spinosa* the protostele of the lower part of the stem has a single central protoxylem, *i e* it is *endarch* and *monarch*, but, higher up, the protoxylem divides into from three to eight groups, which pass to the periphery of the xylem so that the stele becomes *exarch* and *polyarch* (Fig 242, and cf. roots, pp 122, 123).

The **phloem** consists of thin-walled elongated cells, representing the sieve-tubes of higher types. The sieve-

plates are lateral. Outside the phloem is a **pericycle** consisting of either one or two layers of cells The pericycle, however, in *Selaginella* is derived from the same layer of ground-tissue as the endodermis There is no secondary growth

The **ground-tissue** of the stem consists of comparatively thin-walled, more or less prosenchymatous cells, without intercellular spaces (thin-walled prosenchyma, p 48). The **epidermis** also consists of elongated pointed cells, and has no stomata.

§ 28 **The Leaf** is entire, and has a very simple structure Each of the epidermal cells contains, according to species, one or a few large chloroplasts Stomata are usually confined to the lower surface The ground-tissue (mesophyll) is not clearly differentiated into palisade and spongy layers A single vascular strand runs through it This strand is concentric The central xylem is surrounded by a layer of phloem, outside which is an endodermis In some species longitudinal air-spaces are found in the mesophyll

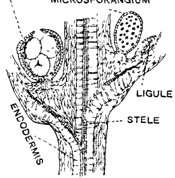


Fig 243 —Part of "Sporangiferous Spike" of Selaginella
(Longitudinal section)

§ 29. **Rhizophore and Root** have on the whole a similar internal structure The stele is mon-arch The root grows by a single apical cell, the rhizophore may have a single cell or a group of cells, according to the species, like the stem

§ 30. **Sporangia and Spores** (Fig. 244)—The sporangium consists of a capsule borne on a short, stout stalk.

The wall of the capsule consists of two layers of cells, and has no annulus. The megasporangium is somewhat larger than the microsporangium The spores as usual have two coats—endosporium and exosporium, the latter being cuticularised. A large amount of food substance is stored up inside the megaspore, consisting chiefly of oil. Owing to the fact that the spores are developed by tetrahedral division (see below) they are pointed at one end.

§ 31 **Development of Sporangium** (Fig 244) —The sporangium is developed from a group of meristematic cells It is first seen as a little papilla-like outgrowth in the axil of a young leaf, close to the apex of the sporangiferous shoot. The outermost layer forms the wall of the sporangium But at an early stage beneath this outermost layer *a row of large cells* can be recognised, and this is the **archesporium.**

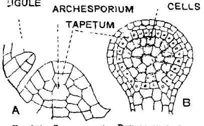


Fig 244 —SELAGINELLA DEVELOPMENT OF SPORANGIUM.
In A only one archesporial cell is shown

The archesporial cells by division form a **tapetal layer** towards the apex of the papilla. In the lower part of the developing sporangium the tapetum is formed from the cells surrounding the archesporium. Then the archesporium, by repeated division, gives rise to spore mother-cells, as in the Fern

So far the development of both mega- and microsporangia is the same, but from this point differences are observed. In the microsporangium the mother-cells separate from each other, and float freely in a nutritive fluid formed by the disorganisation of the tapetal cells Then in all or most of the * mother-cells four *special mother-cells*

* In the latter case the abortive mother-cells serve for the nutrition of the functional ones.

are formed, and each of these gives rise to a microspore in the same way as in the Fern. The microspores are tetrahedrally arranged; they are not formed in the same plane In the megasporangium *one* of the mother-cells increases in size, and produces four megaspores in the same way as a mother-cell produces microspores The other mother-cells are disorganised and serve as nourishment to the developing megaspores Of the four potential megaspores in each megasporangium either all become ripe—and this is the general rule—or one, two or three of them may fail to attain maturity.

At an early stage in development the outermost layer of the papilla divides into two, so that the wall of the sporangium is double. The stalk of the sporangium is formed by division and growth of cells at the base of the original papilla. One layer of tapetal cells persists, so that the wall seems to consist of three layers

§ 32 **Germination of the Spores—Prothalli and Sexual Organs.**—*The germination of the megaspore begins before it is set free from the sporangium.* The nucleus of the spore divides into two. One daughter-nucleus passes to the apex or pointed region of the spore, the other to the basal region

A process of *free cell-formation* then begins. It is most active in the apical region, and there results in the production of a tiny mass of small-celled tissue. In the lower region the process is much less active, and actual cell-formation may not take place there till after the spore has fallen to the ground The cells formed in this region are larger and filled with food-material

The megasporangium ruptures near the apex by a transverse slit, and the spores fall to the ground The megaspore ruptures at the apex by a triradiate fissure which exposes the small-celled tissue immediately underneath On this an **archegonium** is developed, and others are formed later if fertilisation is not effected.

It is evident that the tissue formed as described in the megaspore is the **female prothallus** (Fig. 245) It protrudes slightly, turns green in the presence of light, and

may even develop one or two rhizoids, but it is not set free from the spore as an independent plant, like the prothallus of the Fern or of *Equisetum*. It is nourished by the food-material stored up in the spore. This reduction of the female prothallus to a minute and practically dependent structure should be carefully noticed.

The structure and development of the archegonium (Fig. 246) are practically the same as in the Fern. The

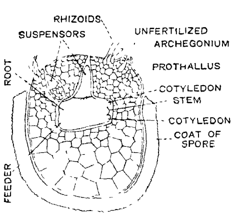


Fig 245 — FEMALE PROTHALLUS OF SELAGINELLA.
(Longitudinal section) An old stage, showing two developing embryos

only difference is that the neck is shorter, consisting of only eight cells, each of the four longitudinal rows of the neck consists of only two cells

The microsporangium is ruptured in the same way as the megasporangium, and the microspores fall to the ground and germinate. The microspore increases in size, and a small cell is cut off at the pointed end (Fig. 247). Then the rest of the spore divides into ten or twelve cells, eight peripheral cells surrounding either two or four central cells (according to the species). The *central* cells undergo further division, and the small cells thus produced are the mother-cells of spermatozoids. In each a

biciliate spermatozoid is formed in exactly the same way as in the Fern

The small cell first cut off represents an extremely rudimentary **male prothallus,** and may be called the *prothallus-cell*. The eight peripheral cells represent the wall of an **antheridium,** inside which the spermatozoids are produced. The extreme reduction of the male prothallus is

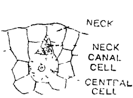


Fig 246 —Young Archegonium of Selaginella

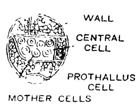


Fig 247 —Germination of Microspore of Selaginella

of great interest, and is correlated with the small size of the microspore The megaspores remain large because of the necessity of providing nourishment for the young sporophyte, and owing to this fact they are able to produce a number of recognisable archegonia

During the course of the above development the exosporium is ruptured. Later the peripheral cells undergo disorganisation and nourish the spermatozoid mother-cells. Eventually the spermatozoids are set free

§ 33 **Fertilisation and Development of Embryo** (Figs 248, 245, 249) —The process of fertilisation is essentially the same as in the Fern and *Equisetum*. But an important difference is that, in *Selaginella*, at the time of fertilisation the ♀ prothallus is still partly enclosed by the megaspore wall. A spermatozoid enters the ovum and fuses with it, the male and female nuclei amalgamating into

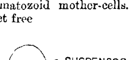


Fig 248 —Segmentation of Oospore of Selaginella (Diagrammatic)

one The **oospore** which is thus formed segments and develops into an embryo sporophyte

The first dividing wall is at right angles to the axis of the archegonium. It divides the oospore into upper and lower cells. The upper cell either remains unicellular or undergoes only a few divisions, the resulting structure being called the **suspensor.** The function of the suspensor is to push the developing embryo down into the tissue of the prothallus, there is no structure corresponding to it in most Ferns.

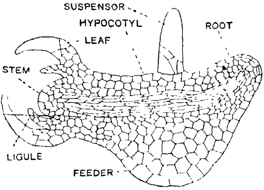


Fig 249 --EMBRYO OF SELAGINELLA
(Longitudinal section)

The segmentation of the lower or *embryonic* cell is comparable to that of the whole oospore in the Fern It is divided by basal, quadrant, and octant walls, formed somewhat irregularly, into eight cells (octants) forming apical (or epibasal) and basal (hypobasal) tiers of four cells each From the apical tier are formed the stem and the two cotyledons; the hypobasal tier gives rise to the hypocotyl In some species (not in *S. spinosa*) the hypocotyl becomes enlarged and forms a massive haustorium or absorbing organ known as the **foot,** or "feeder" The first root is adventitious and is developed from the hypocotyl close to the suspensor.

The development of the embryo in *Selaginella* should be carefully compared with that of the Fern (p 268), and also with that of the Angiosperm (p 404)

The developing embryo grows down into the lower part of the prothallus; the foot absorbs the food-material Eventually the stem and cotyledons escape from the spore and grow above ground, while the first and other adventitious roots pass down into the soil.

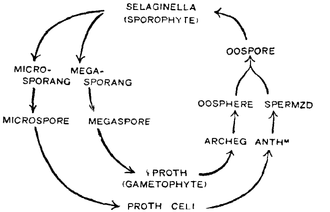


Fig 250 —LIFE-HISTORY OF SELAGINELLA GRAPHICALLY REPRESENTED.

§ 34. **The Life-history** of *Selaginella*, graphically represented in Fig 250, is of great importance, and shows the following points, which should be carefully noticed —

(1) The origin of **Heterospory.** The differentiation of sex has been carried back another stage We not only have two kinds of prothalli, as in *Equisetum*, but these prothalli are developed from spores of two different sizes

(2) The increasing **reduction in size of the gametophytic generation.**

(3) The gradual **loss of independence of the gameto-**

phyte, so that in some species of the genus its whole life is passed as a parasite upon the parent sporophyte

(4) The **reduction in the number of functional megaspores** in each megasporangium In this connexion one species of *Selaginella* (*S rupestris*) is of great interest While in most species all the four spores in a megasporangium come to maturity, in this species three, two, or even only one megaspore may be functional, the others becoming disorganised

If the above facts are well understood, we are in a position to trace **the origin of the seed**, which is a complex structure very characteristic of the Flowering Plants It will be evident that the retention of the gametophyte upon the mother plant means that fertilisation must be effected while the megasporangia (containing the mature female prothalli) are still attached to the plant In *S rupestris* this connexion is in fact kept up till even the *future sporophyte* (embryo) has produced a root and cotyledons At this stage the megasporangium of *S rupestris* is, to all intents and purposes, a "seed." The chief purpose of seed-formation is the protection and nourishment of the future sporophyte, till it is so far advanced that it can strike root and begin an independent life

It is of interest to know that two very ancient fossil plants allied to *Selaginella* also bore seeds. These seeds have been named, respectively, *Lepidocarpon* and *Miadesmia*

The life-histories of Fern, *Equisetum*, and *Selaginella* should be very carefully compared While there are many differences, by reason of which these three types are placed in different classes of the Vascular Cryptogams, the student will recognise that the *general* course of the life-history is very similar. In all three there is a more or less distinct alternation of generations, and equivalent or *homologous* structures occur at the same points in the life-history. The graphical life-histories which have been given will enable the student to grasp more readily the more important homologies discernible

The degeneration of the gametophyte does not cease at this point, but is continued so far that in Flowering

Plants the entire female prothallus remains permanently enclosed in the megaspore, and never contains a trace of chlorophyll. The male cell has to gain access to the hidden archegonium by a special apparatus, the pollen-tube, which is adapted for boring its way through the overlying tissues (See Chapters XVI and XVII)

D. Lycopodium.

§ 35 **General Characters.**—The genus *Lycopodium* (Club-moss), including about 100 species, belongs to the same class of Pteridophyta as *Selaginella* Most of the species are small plants, but some attain a height of 4 or 5 feet, many tropical species are epiphytic The five British species are all found on hills and exhibit marked xerophytic characters The commonest are *L clavatum*, the common Club-moss (Stag's-horn Moss) and *L. Selago*.

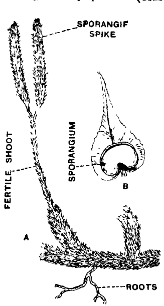


Fig 251 —A, Part of *Lycopodium clavatum*, showing stem, leaves, roots, and sporangiferous spikes, B, A sporophyll and sporangium in surface view

The plant (Fig 251) is the sporophyte In its general appearance it resembles *Selaginella* The firm slender stems, which may be either erect (*L Selago*) or trailing (*L clavatum*), are completely covered with small stiff leaves, usually arranged spirally. The leaves have *no ligule* In some species the branching of the stem is dichotomous, in others it is really lateral although it resembles dichotomy. The roots are adventitious and dichotomously branched

In *L Selago* the stem has a central *cauline* vascular cylinder (protostele) The arrangement of vascular tissue differs in different species, but usually there are a number of rays or plates of xylem with intervening or interpenetrating rays or plates of phloem (Fig 252). The protoxylem

is exarch in some species, as in *Selaginella*, but in other species it is slightly mesarch, that is, there are also a few centrifugal tracheides (tracheides lying to the outside of the protoxylem) There is conjunctive tissue between the xylem and phloem, and the whole vascular cylinder is surrounded by a pericycle and endodermis

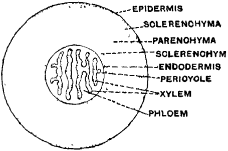


FIG 252 —TRANSVERSE SECTION OF STEM OF *Lycopodium annotinum* (Diagrammatic)

The vascular cylinder of the root is similar to that of the stem The leaves have a single median concentric bundle Root and stem are both developed from a group of apical cells

§ 36 **Sporangia and Spores** (Fig 251) —*Lycopodium* is *homosporous* The sporangia are borne singly, not in the axils of the leaves, but on their upper surfaces near the base In some species, e g *L Selago*, the stems show alternating barren and fertile regions; the sporophylls are not aggregated or specialised in any way and resemble the sterile leaves In other species, e g *L clavatum*, the sporophylls are borne in "spikes" on special branches, and differ in shape from the foliage leaves

The sporangium is developed, as in *Selaginella*, from a group of cells, and when ripe contains a large number of small tetrahedral spores

§ 37 **The Gametophyte.**—The spores on germination produce prothalli which, though small, are the most complex found in the Vascular Cryptogams In *L clavatum* and other species they are tuberous, more or less conical, subterranean bodies, which have no chlorophyll and live saprophytically by means of an endophytic mycorhiza In other species (e g *L Selago*) only the lower subterranean part of the prothallus has this character, the upper part reaches the surface of the soil, develops chlorophyll, and becomes

more or less lobed The prothalli are monœcious and bear both archegonia and antheridia similar to those of *Selaginella*

§ 38 **The Embryogeny.**—The early stages of development are the same as in *Selaginella* (p 419) The hypobasal tier of cells gives rise to the haustorium or **foot**, which may remain small (*L Selago*), or, if the prothallus is deeply buried, may be strongly developed (*L clavatum*) From the apical tier of cells are developed the stem, cotyledon, hypocotyl, and first root In a few species (e g *L clavatum*) there are apparently two cotyledons The first root is adventitious and in some species developed exogenously

§ 39 **Notes on the Life-history.**—*Lycopodium* differs markedly from *Selaginella* in being homosporous The fact, however, that the two genera resemble each other in many respects, by reason of which they are placed in the same group of Vascular Cryptogams, indicates that this difference is not of first-rate importance from the point of view of classification This conclusion is borne out by a general study of the Vascular Cryptogams, both living and fossil, which has shown that while the homosporous condition is undoubtedly the more primitive, the heterosporous condition has originated independently in different groups during the course of evolution

The life-history of *Lycopodium* also illustrates the fact that in homosporous types the gametophyte is well developed The reduction of prothalli, which we have studied in connection with *Selaginella*, is associated with the evolution of the heterosporous condition

CHAPTER XVI.

THE GYMNOSPERMS.

§ 1. **General.**—The Gymnospermous Flowering Plants are not so highly differentiated as the Angiosperms, and in many respects resemble the Vascular Cryptogams, forming as it were an intermediate group. They are large plants, either shrubs or trees, and include the Cycads, the Conifers, and a small group, the Gnetaceæ, whose affinities are doubtful, but which seem to approach nearer to the Angiosperms

Like the Angiosperms, the reproductive organs of the Gymnosperms are aggregated to form flowers, which differ markedly, however, from the flowers of the Angiosperms in the fact that when carpels are present the ovules are borne freely exposed on their upper surfaces. The carpels are not closed up to form ovary, style, and stigma. Hence the name *Gymnosperm* (Gr γυμνος, naked, σπερμα, a seed) * The flowers are always unisexual, the plants usually monœcious, sometimes diœcious (Yew, Juniper, Cycads).

The most important group of the Gymnosperms is that of the **Conifers** or cone-bearing trees, so called because their flowers usually have the characteristic form known as *cones.* The group is well represented in the Indian flora, especially in the Himalayas, where there are enormous areas of coniferous forest containing Pines, Firs, Spruces, Junipers, Yews and Cedars *Cedrus deodara* is the well-known Himalayan deodár tree. The true Pines constitute the genus *Pinus*, of which *P. longifolia* (chíl) and *P excelsa* (kail) are the two best known Indian species. The seeds of *P Gerardiana*, which occurs on the drier inner ranges of the North-western Himalayas and Afghanistan, are the chilghoza of commerce

* Angiosperm from Gr αγγος, a vessel, σπερμα, a seed.

The following description refers to *P. sylvestris*, but most of it will apply equally well to *P longifolia*, the Chīl. The latter differs from *P. sylvestris* chiefly in the much larger size of the ripe female cones, and in having three leaves in each spur instead of two

A. Pinus Sylvestris

§ 2. **External Characters of Pinus.**—The full-grown plant is a large tree Typically it has an elongated **tap-**

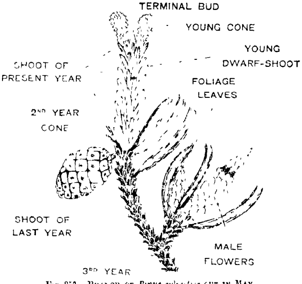


Fig 253 —Branch of *Pinus sylvestris* cut in May
Most of the older dwarf-shoots and foliage leaves removed

root; but frequently the lateral roots are strongly developed and the primary root is comparatively short The main stem is cylindrical and covered with a rugged scaly bark Secondary growth takes place in the same way as in Dicotyledons, and hence the stem tapers towards the apex.

The branches are formed in apparent whorls from lateral buds developed on each parent axis These are formed in the axils of scale-leaves, at the end of each year's growth. This regular development of branches gives the tree a very symmetrical appearance, which is, however, frequently spoilt owing to the loss of many of the branches In addition to the ordinary branches, which, as they grow indefinitely, are called *shoots of unlimited growth*, there are numerous **dwarf-shoots** or *shoots of limited growth* (Fig 253). These also arise in the axils of brown scale-leaves borne on the main branches.

The leaves are of two kinds —(*a*) the **scale-leaves** just mentioned, which are the *only* ones borne on the shoots of unlimited growth, and which are also present on the dwarf-shoots; (*b*) green **acicular foliage leaves,** popularly called "*needles*," which occur solely upon the dwarf-shoots; they are not borne directly on the shoots of unlimited growth.

The dwarf-shoots, with their clusters of green leaves, are called "*spurs*" The number of green leaves in each cluster varies according to the species of *Pinus*. In *P. sylvestris* there are two, and the dwarf-shoots together with their leaves are termed "bifoliar spurs." These persist for a number of years, so that the tree is an evergreen When they fall off, as they eventually do, it is the dwarf-shoots which are shed, and the leaves fall with them

Pinus has no power of vegetative reproduction

The presence of a tap root is characteristic of Gymnosperms. Many, e g *Picea*, the Spruce, have leaves and shoots of one kind only The branching is axillary, but buds are not formed in the axils of all the leaves. No buds are formed in the axils of the foliage leaves of *Pinus*.

§ 3. **Structure of the Stem.**—In the general *arrangement* of tissues the stem of the Conifer closely resembles that of the Dicotyledon It is eustelic (p 102) At the apex there is a small-celled **meristem,** in which, however, there is no dermatogen distinct from periblem; cortex and epidermis originate from a common layer (periblem)

The **bundles** in the primary condition (Fig 254) are common, conjoint, collateral, and open, and form a ring in transverse section The primary bundles in *Pinus* lie close together, so that the medullary rays between them are extremely narrow. The **ground-tissue** is differentiated into pith, cortex, and medullary rays. The pericycle is parenchymatous, and therefore cannot readily be distinguished from the cortical tissue; the same is the case with regard to the endodermis, which is the innermost layer of cortical cells. The primary bundles have therefore no pericyclic sclerenchyma or hard bast.

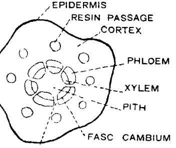


FIG 254 —STEM OF PINUS. (Transverse section Diagrammatic)

Large **resin-passages** are present in the cortex, each surrounded by a layer of glandular secreting epithelial cells As the transverse section of the young stem cuts through the bases of the dwarf-shoots its outline is irregular A somewhat lignified hypodermal layer may be recognised in the outer cortex

Secondary growth is effected in exactly the same way as in Dicotyledons (pp 103-109), the cambium ring giving rise to secondary wood and phloem, and the phellogen to cork and bark The **phellogen** or cork-cambium originates in the cortical tissue near the surface, though not in the outermost layer, and, later, there is a repeated formation of tangential lines of phellogen cutting off strips of scaly bark (p 109).

§ 4 **The Tissues of the Stem** (Figs 255-257) —The close resemblance to Dicotyledons will be recognised The differences, however, are considerable, the vascular tissues especially being of simpler character. The wood or **xylem**

has *no true vessels*, but consists of tracheides (cf V Cryptogams) with very typical bordered pits The **protoxylem** consists of annular and spiral tracheides Small resin-passages are present in the primary and secondary wood, each with its lining epithelial layer The **phloem** consists of sieve-tubes and phloem parenchyma, *there are no companion cells* (cf V. Cryptogams) The sieve-tubes consist of elongated, more or less pointed (prosenchymatous) cells, with lateral sieve-plates on the radial walls

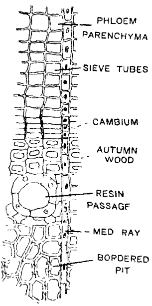


Fig 255 Stem of Pinus
Portion of a transverse section after secondary growth

The structure of the **medullary rays,** however, is more complex than that of Dicotyledons (Figs 256, 257) The rays in the secondary wood consist partly of cells containing starch, partly of *tracheides* running radially. These tracheides allow for the radial diffusion of watery fluids through the wood, and thus make up for the want of wood-parenchyma In the secondary phloem the rays consist partly of starch-containing cells, partly of cells with albuminous contents The medullary rays vary much in size; the smallest are only two cells high and one cell wide

Figs. 255-257 show transverse and longitudinal sections of the wood A radial longitudinal section runs parallel to the medullary rays in the region in which it is taken, while a tangential longitudinal section cuts *across* them. This will explain the difference in the appearance of the medullary rays in the two sections (Figs 256, 257)

The differences in the appearance of the bordered pits are due to the fact that the tracheides are four-sided, two of the sides being approximately radial and two tangential, and that the bordered

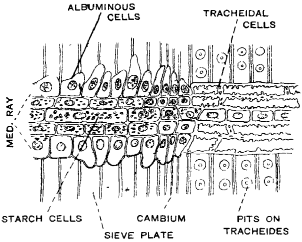


Fig 256 – Radial Longitudinal Section of Stem of *Pinus*.
The section is taken at the junction of secondary wood and phloem

pits are confined to the radial walls Thus, in radial section, the radial walls are not cut through and the pits are seen in surface view, while in tangential section the radial walls are cut through and the pits are seen in section (Fig 257).

§ 5 **The Root.**—The growth and general arrangement resembles that of Dicotyledons. The **apical meristem** shows periblem and plerome layers, but there is no dermatogen layer, the root-cap and piliferous layer being derived from the periblem In *Pinus* there are from two to six Y-shaped **xylem** bundles, and an equal number of **phloem** bundles alternating with them; there is a resin-passage between the arms of each Y, and a pith may be present. The arrangement, however, is not characteristic of Conifers as a class In most cases the stele is di-arch (or tri-arch), and a pith is absent.

In Gymnosperm roots the **pericycle** *consists of several layers*, but there is a single-layered *endodermis*. **Secondary growth** takes place as in the roots of Dicotyledons The *phellogen* originates in the outermost layer of the pericycle. The wood and phloem have the same structure as in the stem **Lateral roots** are developed from the second layer of the pericycle, the outermost layer covering them helps in the formation of the digestive sac which enables them to burrow outwards through the cortex. The roots of *Pinus* have a mycorhiza, and root-hairs are scantily developed



FIG 257 —SECONDARY WOOD OF PINUS Portion of a tangential longitudinal section

§ 6 **The Leaf.**—Fig 258 shows a transverse section of the foliage leaf. The **epidermis** consists of extremely thick-walled cells with a strong cuticle Stomata are developed all over its surface. The guard-cells are sunk beneath the level of the epidermis, so that there is an outer cavity leading down to the stoma. Beneath the epidermis there is a fibrous sclerenchymatous **hypodermis** interrupted beneath the stomata

The parenchymatous **mesophyll** is not differentiated into palisade and spongy layers, it consists of thin-walled cells, whose walls show numerous plate-like infoldings of cellulose projecting into their cavities The presence of these is probably connected with the feeble development of air spaces in the leaf, for they increase the internal surface of the cell-wall, and hence also the excreting and absorbing surface of the protoplasm. The cells contain numerous chloroplasts and starch-grains. In the meso-

phyll, immediately under the hypodermis, are a number of *resin-passages*, each with a thin-walled epithelial layer and an investing strengthening layer of sclerenchyma

In the middle of the leaf there is a conspicuous **endodermis** surrounding a many-layered **pericycle,** in which two **vascular bundles** are imbedded. The bundles are collateral, the xylem facing towards the flat upper surface

In addition to the pericyle the space between the vascular bundles and the endodermis is occupied by a peculiar

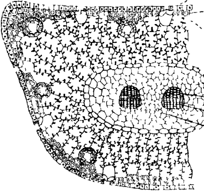


Fig 258 —Transverse section of Leaf of Pinus

tissue called **transfusion tissue,** which is characteristic of the leaves of Gymnosperms. It consists of—(*a*) parenchymatous cells, rich in protoplasm, proteid, and starch, and called *albuminous cells*, (*b*) cells with bordered pits and no contents, resembling tracheides and called *tracheidal cells*. This tissue helps in the transference of nutritive solutions, and thus makes up for the poor development of vascular tissue. The tracheidal cells serve for the passage of inorganic solutions from the xylem to the mesophyll; the other cells for the diffusion of elaborated compounds from the mesophyll to the

phloem. In addition to the transfusion-tissue, a number of fibres are developed in the pericycle near the bundles.

The narrow acicular form of the leaves, their thick cuticle, the sunken stomata, the presence of a strong hypodermis, the simple vascular system, are marked xerophytic characters, all tending to reduce transpiration to a minimum.

§ 7 **The Male Flowers** (Fig 253) appear early in the year—about the beginning or middle of May. They are produced in the axils of scale-leaves at the bases of the developing shoots of the same year, but not on all the shoots. They form a spike at the base of the shoot, and the latter, as it continues to grow, develops ordinary dwarf-shoots in the axils of the upper scales In other words, the male flowers are produced at the base of the shoot in place of dwarf-shoots, and are homologous with them.

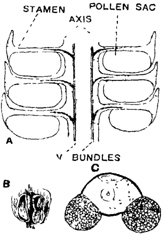


Fig 259 —MALE FLOWER OF PINUS.
A, Part of a median longitudinal section (diagrammatic), B, Stamen (under surface), C, Pollen-grain (two-celled stage, highly magnified)

Each male flower (Fig 259) consists of a somewhat elongated axis which corresponds to the thalamus, and which bears a number of spirally arranged scaly leaves. On the under side of each scale **two pollen-sacs** are developed and these are filled with **pollen-grains.** The scales of the male flower, therefore, are **stamens.** The pollen-grains are *at first* unicellular bodies with exosporium or exine, and endosporium or intine (p. 237) On each side of the pollen-grain the exosporium is inflated with air, forming two balloon-like expansions (Fig 259, c).

The male flowers differ from the flowers of Angiosperms in that (*a*) the axis which corresponds to the thalamus is elongated, (*b*) the stamens are less highly differentiated, showing no distinction into filament and anther, (*c*) there are two instead of four pollen-sacs. It should also be noticed that the essential organs only are present. There is no perianth, but a few sterile scales occur at the base of the male flower.

Most Conifers have male flowers like those of *Pinus*. The number of pollen-sacs, however, differs in different types.

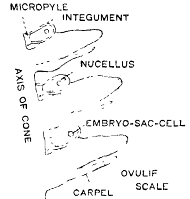


FIG 260 —YOUNG FEMALE CONE OF PINUS. (Part of a longitudinal section diagrammatic.)

§ 8 **The Female Flowers,** or cones (Fig 258), are developed laterally in the axils of scale-leaves at the apices of the young elongated shoots. They are usually borne on shoots which do not bear male flowers, and take the place of shoots of unlimited growth. There may be from one to four on each shoot.

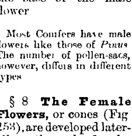


FIG 261.—SCALES OF FEMALE CONE
From above and below (Carpel-scale = cover scale).

The female flower (Figs 260, 261), if examined at this early period, is found to be a small, reddish structure consisting of a stout central axis, bearing scales of two kinds —(*a*) small scales arranged spirally and developed directly on the axis; these are called the **bract-** or **cover-scales**; (*b*) rather stouter scales developed one on

the upper surface of each bract-scale; these are called **ovuliferous scales,** because each bears two ovules on its upper surface As the ovules afterwards give rise to seeds, the ovuliferous scales are also called "seminiferous scales." Each bears at its apex a little protuberance called the *apophysis*

To compare this with the Angiosperm, the so-called bract-scale is regarded as equivalent to (i e the homologue of) a carpel, and should, therefore, be called a *carpellary* scale, while the ovuliferous scale is a large **placenta.** Here again the elongated axis should be noticed. The most important point of difference, however, is that the carpels do not assume the form of a closed ovary, with a style and stigma.

The female cones of the Spruce and Larch closely resemble those of *Pinus* In the Larch the bract-scales are considerably larger In the Cypress and the "Tree of Life" (*Arbor vitae*) the carpellary scales of the female cone do not bear ovuliferous scales a number of ovules are borne directly on the surface of the scales, which are arranged, not spirally, but in opposite decussate pairs.

There are other views entertained with regard to the homologies of the female cone of *Pinus* The bract-scale by some is regarded as really a bract, and the ovuliferous scale with the two ovules, as a female flower of a very rudimentary type According to this view the female cone would be, not a single flower, but an inflorescence

§ 9. **Structure of the Ovule** (Fig 260) —In the young female cone just described, the ovule consists of a small-celled mass of tissue, the **nucellus,** surrounded by a single integument Towards the base of the nucellus, one large cell is developed called the **embryo-sac-cell,** homologous with the embryo-sac of the Angiosperm There is a wide gaping *micropyle* directed towards the axis of the cone

§ 10. **Comparison with Vascular Cryptogams.**—Having explained in the preceding sections the homologies between *Pinus* and the Angiosperm, we may now make the connecting link in the other direction by giving the homologies which can be recognised between *Pinus* and the Vascular Cryptogams.

They may be stated briefly thus —

(*a*) The **plant (Pinus)** is the *sporophyte*.

(*b*) **Pollen-grain** = *microspore*,
Pollen-sac = *microsporangium*;
Stamen = *microsporophyll*,

(*c*) **Embryo-sac-cell** = *megaspore*;
Nucellus = *megasporangium*;
Carpel (bract-scale) = *megasporophyll*.

These homologies should be very carefully noticed. In the description of the flowers of *Pinus* either set of terms may be used. The terms pollen-grain, pollen-sac, etc., were given to these structures before their homologies were revealed by a study of their development and position in the life-history, and by a careful comparison with such types as *Selaginella*

The student must clearly comprehend that the recognition of homologies is based on a comparative study of development. To emphasise this we shall now describe the development of pollen-sac and ovule in *Pinus*; it will be found to be essentially similar to the development of micro- and mega-sporangia of *Selaginella*.

§ 11 **Development of Pollen-Sac and Ovule.**—The pollen-sac is developed *from a group of cells* (cf *Equisetum* and *Selaginella*) on the under surface of the young stamen The wall of the pollen-sac is formed from the superficial or epidermal layer; it remains single Several hypodermal cells, forming the **archesporium**, begin to divide rapidly Tapetal cells are segmented from them towards the wall of the pollen-sac, and the remaining central portion forms a mass of **pollen-** or **spore-mother-cells.** Each mother-cell gives rise, exactly as in *Selaginella*, to four microspores or pollen-grains The pollen-grain has the structure of a spore; its outer coat corresponds to the exosporium, its inner one to the endosporium. The tapetal cells are disorganised during the development of the pollen-grains.

The **ovule** arises as a small cellular protuberance on the

upper surface of the young ovuliferous scale. It increases in size and becomes the nucellus The single integument arises from the base of the nucellus and gradually invests it. At the apex of the young nucellus a single hypodermal cell, the **archesporium**, can be recognised. This begins to divide and forms **tapetal cells** towards the apex of the nucellus The archesporium proper remains unicellular, and owing to continued division of the overlying tapetal and nucellus cells it comes to lie near the base of the nucellus It eventually divides into four cells (tetrad division), and one of the resulting cells becomes the embryo-sac-cell or megaspore The only point to be noticed here is that there is only one spore-mother-cell and only one megaspore develops

The nucellus is probably equivalent to the proper wall of the megasporangium The integument is by many regarded as of the nature of an *indusium* (cf the Fern), in this case surrounding a single sporangium, it is not represented in *Selaginella*

§ 12 **Pollination.**—As in Angiosperms, the pollen-grains or microspores have to be transferred to the neighbourhood of the embryo-sac or megaspore In *Pinus* this is effected by means of the wind, the transference being facilitated by the balloon-like expansions of the exosporium already described. *Pinus*, therefore, is *anemophilous*

Pollination takes place towards the end of May or beginning of June At this period the scales of the female cone open out, and separate from each other Much of the pollen is wasted, but some of the grains are blown between the scales of the female cone and fall near the ovules A mucilaginous secretion is given out from the micropyle In this the pollen-grains are entangled, and, as the drop is sucked in, they are drawn down the micropyle and finally come to rest on the apex of the nucellus In the Gymnosperms pollination consists in the transference of the pollen-grains, not to a stigma as in Angiosperms, but directly to the surface of the nucellus The scales of the female cone close up after pollination

§ 13 **Male Gametophyte.**—If the pollen-grain is really a microspore we should find it giving rise on germination to something equivalent to a male prothallus. At first the pollen-grain is unicellular. Even before it leaves the pollen-sac division begins, and it is completed on the surface of the nucellus. Two very minute rudimentary

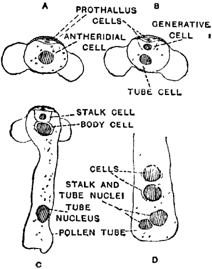


Fig 262.—*Pinus* STAGES IN THE GERMINATION OF THE POLLEN GRAIN
The pollen is shed at the stage A. D is a stage shortly before fertilisation occurs

cells, the **prothallus-cells**, are cut off on one side. The remainder, which is the antheridial cell, then segments into a small **generative cell** and a large **tube cell** (Fig. 262, A).

Comparing this with the germination of the microspore in *Selaginella*, there is an obvious suggestion that the small prothallus-cells represent a very rudimentary or reduced **male prothallus.** The antheridial cell is so called because, as will presently be explained, it produces

the male sexual cells, and is hence equivalent (although only functionally) to the antheridium of the Vascular Cryptogam, the male sexual cell being the equivalent or homologue of the spermatozoid The **male cells**, however, are not motile, *i.e.* they are not spermatozoids

In the further germination of the pollen-grain on the apex of the nucellus, the exosporium bursts open and the large vegetative cell protrudes and elongates to form a slender pollen-tube (Fig. 262, c). This is not represented in *Selaginella*, its development in Phanerogams, as will afterwards be explained (p 461), is an adaptation to entirely different conditions The pollen-tube grows down into the tissue of the nucellus. Its destiny will be traced presently

§ 14 **Growth of Female Cone. The Female Gametophyte.**—At first, as we have seen, the female cone is comparatively small, and the ovule consists simply of the integument, the nucellus, and the embryo-sac-cell or megaspore Although pollination is effected at this stage, fertilisation does not take place in *Pinus* till about a year later—some time in June of the second year. This, however, is not characteristic of Gymnosperms; in most of them fertilisation is effected in the same year as pollination

In *Pinus*, during this protracted interval between pollination and fertilisation, many important changes go on in the ovule and in the cone as a whole The cone increases in size and becomes green. During the winter these green cones are found at the apices of the shoots, just below the terminal winter bud This increase in size is due to the enormous growth of the axis and of the ovuliferous scales. The carpellary scales remain small, and are completely concealed The growth is continued rapidly in the second year (Fig 253) At the time of fertilisation the cones are large green structures, the rhomboidal areas on their outer surface being the outlines of the apices of the ovuliferous scales

Inside the ovule the embryo-sac-cell becomes much larger, and by *free cell-formation* there is formed *inside it*

a mass of thin-walled parenchymatous tissue. If this process be compared with the germination of the megaspore in *Selaginella*, there will be no difficulty in recognising that the tissue formed in the embryo-sac-cell is the **female prothallus** (Fig 263).

Practically, the only important difference is that the megaspore in *Pinus* is not set free from the megasporangium, as it is in *Selaginella*. But even in *Selaginella*,

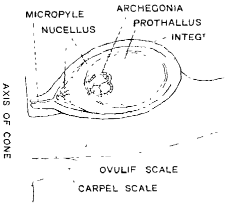


Fig 263.—OVULE OF PINUS.
(Longitudinal section—about the time of fertilisation)

it will be remembered, the germination of the megaspore begins inside the sporangium.

The female prothallus in *Pinus* is enclosed in the nucellus. It has neither chlorophyll nor root-hairs. At its micropylar end are developed two or three **archegonia.** This completes the evidence of homology. The archegonium consists of a *venter* and a short *neck* **Oosphere** and *ventral canal-cell* are present, but there is no neck-canal-cell. The protoplasm of the oosphere presents a frothy appearance, owing to extensive vacuolation, it has no cell-wall. Except that no neck-canal-cell is formed, the development is essentially the same as in the Fern or *Selaginella.*

§ 15 **Fertilisation.**—In the first year the growth of the pollen-tube is arrested after it has penetrated a short distance into the nucellus In the second year it again begins to grow Some time in April the generative cell (§ 13) divides into two (Fig 262, B)—a barren cell called the **stalk-cell**, and a **body-cell.** The protoplasmic contents and nuclei of the large tube-cell, the stalk-cell, and the body-cell, all pass down to the apex of the pollen-tube

In the pollen-tube the naked body-cell divides into two cells, the *male gametes* The pollen-tube ultimately reaches and enters an archegonium One of the gametes only is concerned in the act of fertilisation It passes from the pollen-tube into the ovum, and its nucleus together with a small amount of cytoplasm fuses with the nucleus and cytoplasm of the ovum The fertilised ovum forms a cell-wall and becomes the **oospore.**

§ 16. **Development of Embryo** (Fig. 264) —The fertilised nucleus passes to the lower end of the oospore, where by repeated karyokinetic division it gives rise to four nuclei, all lying in one plane at right angles to the long axis of the oospore. Three further divisions result in the production of four tiers, each of four nuclei All the nuclei, except those of the uppermost tier, are separated by cell-walls. The three lower tiers are called respectively (from below upwards) the embryo tier, the suspensor tier, and the rosette tier, and the whole structure is called the **pro-embryo.** Only the lowest tier, however, gives rise to the embryos, the other three tiers helping in their nutrition. The suspensor cells elongate enormously, pushing the embryo deep into the food-laden ♀ prothallus or endosperm During this elongation as a rule the four suspensors diverge, each bearing at its tip one of the four embryo cells. By rapid division of the latter four potential embryos are produced.

This is an example of *polyembryony* (see p 271); it is very characteristic of Coniferæ. As more than one oosphere may be fertilised, many potential embryos may be present in one ovule. Only one, however, develops, the others die off Occasionally the suspensors do not

diverge, and a single embryo is produced from the four cells of the embryo tier.

The embryo which is developed consists of a **primary root,** a tiny **plumule,** and a *number of* **cotyledons.** The whole of it is derived from the embryonal mass, the suspensor taking no part in the development

It should be carefully noticed that the **endosperm** is simply the tissue of the female prothallus laden with food-material which diffuses into it from the placenta.

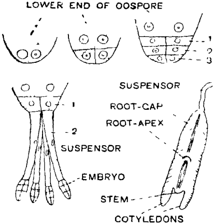


Fig 264 —SEGMENTATION OF OOSPORE AND DEVELOPMENT OF EMBRYO OF PINUS Only half the number of nuclei, cells, and rows of cells is, of course, shown in the early stages

The nucellar tissue is almost entirely crushed and disorganised owing to the expansion of the endosperm and embryo A thin layer of it persists, and contains food-material, forming a small amount of *perisperm* (p 272).

§ 17 **Seed and Fruit.**—Thus, as in Angiosperms, a seed is formed (Fig 265) The integument of the ovule becomes the **testa.** The seed contains, not only endosperm, but also a small amount of perisperm. The **embryo** is straight and lies in the middle of the endosperm

The suspensors disappear. The seed has a thin membranous *wing*, which assists in its dissemination. The wing is derived from the surface of the placenta, not from the testa.

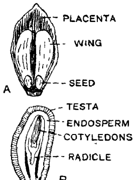


Fig 265.—SEED OF PINUS.
A, Surface view, B, Longitudinal section. The perisperm is not shown

The female cone, when it reaches maturity *in the third year*, is dry, brown, and woody. The scales (placentas) gape apart and allow the seeds to escape. The cone, as a fruit, is necessarily quite different from Angiospermous fruits, seeing that there is no ovary.

The fruits of most Conifers are dry, woody cones. In some, however, the carpels become fleshy and form a berry-like fruit *e g* in the Juniper.

§ 18. **Germination of Seed.**—The cotyledons of *Pinus* may become green while still enclosed in the seed-coat. They gradually absorb the endosperm, and are epigeal, the seed-coat being carried by them above ground. The primary root passes downward and forms the tap-root system. The first year's shoot, formed by the elongation of the plumule, has no scale-leaves or dwarf-shoots; it has acicular green leaves, spirally arranged, thus indicating what was probably the primitive leaf arrangement.

The life-history of *Pinus* may be graphically represented as in Fig. 266.

B. THE YEW

§ 19 **General Characters.**—The Yew (*Taxus baccata*) is an evergreen tree, with massive trunk and spreading branches, which may reach a height of 30 or 40 feet. During its growth branching occurs from the base, and the

branches fuse together to form the compound columnar trunk characteristic of the tree. In the Himalayas, where the tree grows quite plentifully, it may attain a height of 100 feet.

The small narrow, dark-green leaves (Fig 268) are borne singly and are closely set on opposite sides of the branches.

Resin passages are wanting, and the tracheides possess spiral thickening bands in addition to typical circular bordered pits like those of *Pinus*.

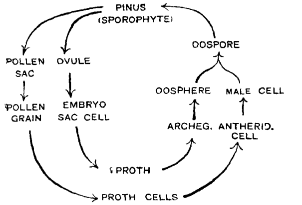


Fig 266 —LIFE-HISTORY OF PINUS.
Graphical representation (Cf Figs 207, 209, 219)

The Yew is diœcious The male and female flowers (Fig 267) are developed on different trees in the axils of leaves of the previous year. They appear in February or March, and are found on the under side of the branches.

§ 20. **The Flowers** (Fig 267) —The *male flower* consists of an axis bearing 6-10 stalked peltate stamens. On

the under side of the head of each stamen are 5-9 pollen-sacs. The pollen-grains have no lateral expansions of the exine At the base of the male flower are a number of scale-leaves, which at first cover over and protect the young stamens

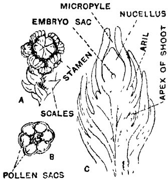
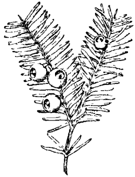


FIG 267 —FLOWERS OF YEW
A, Male flower, B, Single stamen seen from below, C, Longitudinal section of bud containing female flower

The *female flower* is not a cone A bud, bearing a number of overlapping scales, arises in the axil of a leaf of the previous year The apex of this bud undergoes no further development, but in the axil of one of the upper scales there arises a very short lateral shoot which bears a few scale-leaves, and ends in a single ovule Thus the female flower consists of *a single ovule* terminating a short axillary shoot The structure and development of the ovule are similar to those of *Pinus*

§ 21 **Embryo and Seed.**—Pollination and fertilisation are effected as in *Pinus*, but in the same year Only one embryo is developed from the oospore. During development a cup-shaped structure grows up from the base of the ovule (Fig 267) This is the **aril.** It becomes fleshy and forms the red investment of the ripe seed The "fruit" or "berry" of the Yew is simply a seed with an investing aril (Fig 268) and is distributed by birds


FIG 268 —TWIG OF YEW WITH "FRUITS"

C. Cycas.

§ 22 **General Characters.**—The present-day Cycads, comprising only 9 genera with about 75 species, are descended from a much larger group of plants which probably flourished all over the world in past geological times The best-known genus is *Cycas*, of which several species occur in India, including *C. revoluta*, and *C. circinalis* the pith of which yields a kind of sago

The stem of a Cycad is short and stout, either cylindrical, or more or less swollen and tuberous Branching sometimes occurs, especially in old plants, but is not common A tap-root system is developed At the top of the stem are alternating zones of foliage leaves and scale-leaves, the latter protect the former in the bud condition The foliage leaves are large and usually pinnate, occasionally bipinnate, they persist for several years. The lower part of the stem is covered with leaf-scars

The stem of *Cycas revoluta* is cylindrical, resembling that of a tree-fern, the leaves are pinnate and, like the leaves of ferns, have circinate ptyxis. The fern-like habit of the plant is especially noticeable

In the young stem there is a ring of collateral bundles. Secondary growth occurs The wood contains tracheides only. The medullary rays are usually very broad Mucilage ducts are characteristic of the group

§ 23 **The Flowers** are borne on different plants. The male flower of *Cycas*, as of other Cycads, is a cone borne *terminally* at the apex of the stem The growth of the stem is continued by a lateral bud, and is therefore sympodial. The male cone consists of an axis bearing a large number of spirally arranged scales (stamens) on the under surface of which are numerous pollen-sacs (microsporangia) *arranged in sori* (Fig 269, B)

In all the genera except *Cycas* the large female cones are borne similarly at the apex of the female plants, each scale (megasporophyll or carpel) of the cone bearing two marginal ovules But in *Cycas* the female flower

is peculiar, and gives evidence that the genus is a very primitive one. It consists of a rosette of pinnate sporophylls or carpels, developed in place of foliage leaves The rosettes of sporophylls and foliage leaves alternate with each other as growth goes on. The growth of the axis is continued *through the female flower*. The pinnate sporophylls (Fig. 269, A) are smaller than the foliage leaves, have no chlorophyll, and are covered with hairs. The lower leaflets of the sporophyll are replaced by *large* ovules, two to eight in number.

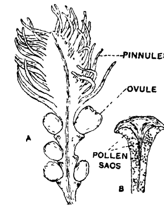


Fig 269 —SPOROPHYLLS OF *Cycas revoluta* A, CARPEL, B, STAMEN

§ 24. **Structure of Ovule.**—Like the ovules of *Pinus* and *Taxus*, the Cycad ovule consists of a nucellus surrounded by an integument which is perforated at the apex by a micropyle. But in the Cycads the nucellus is fused to the integument for most of its length. Moreover, the apex of the nucellus is hollowed into a so-called **pollen-chamber.** The megaspore mother cell divides into a row of 3-4 potential megaspores, only one of which matures into a functional megaspore (embryo-sac). This produces, as in *Pinus*, a ♀ prothallus (endosperm) completely enclosed by the nucellus and bearing archegonia at its apex During development the pollen-chamber containing the germinating pollen-grains becomes deeper and deeper till its floor reaches the ♀ prothallus, and the archegonia now open into it

§ 25. **Pollination and Fertilisation.**—The pollen-grains are carried to the ovules by the wind. They are caught by a mucilaginous secretion from the micropyle, and are sucked into the pollen-chamber.

The pollen-grains, which are devoid of wings, germinate in much the same way as in *Pinus*. But the two male cells produced from the body-cell, instead of being motionless, are ciliated and motile, *they are in fact spermatozoids*. By the time the spermatozoids are fully developed, the pollen-chamber has penetrated right through the nucellus and reached the archegonia. One of the pollen-tubes then bursts and the spermatozoids, together with a drop of watery fluid, are set free, and make their way to the archegonia. The actual process of fertilisation takes place as in Vascular Cryptogams. The pollen-tube does not enter the archegonium.

Spermatozoids have been found in all Cycads examined, and also in *Ginkgo biloba*, the Maiden-hair Tree of China and Japan, the only remaining representative of a family of Gymnosperms well represented in earlier times. Their discovery, which is recent, illustrates in the most striking way the accuracy of the conclusions which, on other evidence, had been arrived at with regard to the homologies between the Gymnosperms and Vascular Cryptogams.

CHAPTER XVII.

HOMOLOGIES IN ANGIOSPERMS

§ 1. The Sporophyte in the Angiosperm.—We are now in a position to correlate the main facts in the life-history of the Angiosperm with those of the Vascular Cryptogam and Gymnosperm From what has been said in the preceding chapter the following homologies will be evident:—

(*a*) The **Angiospermous plant** is the *sporophyte*.

(*b*)	**Stamen**	= "*microsporophyll*";
	Pollen-sac	= *microsporangium*,
	Pollen-grain	= *microspore*.
(*c*)	**Carpel**	= "*megasporophyll*";
	Nucellus	= *megasporangium*;
	Embryo-sac	= *megaspore*.

The sporophyte in the Angiosperm is still more highly differentiated than that of the Gymnosperm As in the Gymnosperm, the sporophylls are aggregated to form **flowers.** In Angiosperms the flowers have undergone extreme specialisation. In addition to the sporophylls or essential organs they usually have accessory structures—the floral envelopes or **perianth**—which play an important part in the production of seed.

To complete the evidence of homology, we may briefly describe the development of pollen-sac and ovule of the Angiosperm. It is essentially similar to the development in Gymnosperms and Vascular Cryptogams.

§ 2. **Development of the Pollen-sac** (Fig. 270).—The stamen in the Angiosperm arises as a protuberance on the thalamus It consists of meristematic tissue, and soon shows a distinction into filament and anther. The two

anther-lobes can be recognised at an early stage, and a procambial strand makes its appearance in the region of the connective.

In *each* anther-lobe, two little groups of periblem cells lying immediately beneath the dermatogen begin to divide. They form usually three layers of cells underneath the dermatogen layer. The outermost of the three layers becomes the **fibrous layer** (p. 236) of the pollen-sac. The

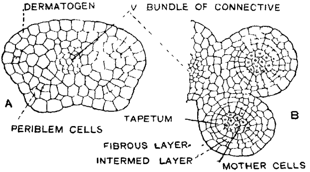


Fig. 270.—DEVELOPMENT OF POLLEN-SACS IN ANGIOSPERM. Transverse sections of young anthers.

innermost layer consists of large granular cells and forms a **tapetum**; together with the intermediate layer it is disorganised during the development of the pollen-grains The remaining cells of each meristematic group constitute the **archesporium.**

Thus in each anther-lobe there are two archesporia The tapetal layer completely surrounds each archesporium The archesporial cells divide in the usual way to form spore- (or pollen-) mother-cells. In Dicotyledons, the **special mother-cells** are formed in much the same way as in the case of the Fern (p 399), but in Monocotyledons they are formed by ordinary cell-division, *i e.* the mother-cell divides into two and then these two into four. The microspores or pollen-grains in both are formed in the usual manner.

§ 3 **Development of Ovule** (Fig 271) —The **nucellus** arises as a tiny cellular protuberance on the placenta and gradually increases in size The **integuments** arise, one after the other, as outgrowths from the base (chalaza) of the nucellus. This basal region also elongates to form the *funicle*

At an early stage the **archesporium** is recognised as a single *hypodermal* cell at the apex of the young nucellus

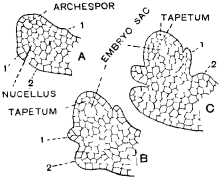


FIG 271 —DEVELOPMENT OF AN ANATROPOUS OVULE
1, 2, = 1st and 2nd integuments

It *usually* divides into two—an upper *tapetal cell* and a lower cell, the *archesporium*. The tapetal cell *may* divide again. The archesporial cell functions as a spore-mother-cell, in typical cases it divides into a row of four potential megaspores, the lowest of which becomes the **embryo-sac** or megaspore, the other three, called "*cap-cells*," showing no further development In the primitive dicotyledonous genus *Casuarina*, however, all four become embryo-sacs

The embryo-sac or megaspore is at first a typical cell with a single nucleus, but before fertilisation a process of free cell-formation takes place The nucleus divides karyokinetically into two. One daughter-nucleus passes to the micropylar end, the other to the chalazal end of the embryo-sac. Each by further division gives rise to four

nuclei Three of the nuclei at the micropylar end become surrounded by protoplasm, and form the **oosphere and synergidæ** or egg-apparatus, three at the chalazal end are surrounded by protoplasm and cell-walls, and form the **antipodal cells.** A nucleus remains at each end. These are called *polar nuclei*, they pass to the centre of the embryo-sac and fuse to form the **secondary nucleus.** The second male cell fuses with the polar nuclei or with the resulting secondary nucleus (p 268). Thus the endosperm-nucleus is the result of "triple fusion" of nuclei

§ 4 **The Gametophyte in the Angiosperm.**—The male gametophyte is completely reduced The vegetative and generative cells of the pollen-grain (p 267) represent all that there is of male prothallus and antheridium The vegetative cell is probably equivalent to the peripheral cells forming the wall of the antheridium in Selaginella Otherwise the antheridium of the Vascular Cryptogam is represented only by a generative cell which, as in Gymnosperms (p 391), divides to form two gametes, corresponding to the spermatozoids.

Remembering the process of free cell-formation which takes place in the megaspore of Gymnosperms and of *Selaginella*, we must recognise that the formation of antipodal cells and egg-apparatus in Angiosperms is, as it were, an attempt at the formation of a *female prothallus.* The process, however, comes abruptly to an end After fertilisation it is continued (see p 271), and leads to the formation of the endosperm tissue. The endosperm tissue is the female prothallus *formed after fertilisation.* The secondary nucleus may be considered as a resting nucleus set apart before fertilisation to continue the formation after fertilisation. The antipodal cells are usually regarded as a rudimentary formation of prothallus tissue. The egg-apparatus may perhaps represent three *reduced* archegonia. The female *organs* or archegonia themselves are lost, but their essential cells (oospheres) have persisted. Two of these, the synergidæ, are functionless In a few plants, however, one or other of the synergidæ may be fertilised.

The life-history of the Angiosperm may be represented as in Fig. 272.

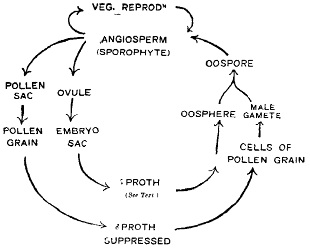


Fig 272.—Life history of Angiosperm graphically represented

§ 5. **The Flower.**—We must now bring distinctly before the student the fact that the flower is simply a specialised reproductive shoot (see p 8) bearing an aggregation of sporophylls *Morphologically*, the flower is not a structure peculiar to the Phanerogams It has its morphological equivalent, *i e* its homologue, amongst the Vascular Cryptogams, *e g.* the sporangiferous heads of *Equisetum* and *Selaginella* Many, indeed, have extended the application of the term *flower* to these and similar structures amongst the Vascular Cryptogams On this view, the term *Flowering Plant* applied to the Phanerogam would be a misnomer. Others, however, would restrict the term "flower" to the Phanerogams This could be done by giving the following definition.—The flower is a specialised reproductive shoot bearing sporophylls and sporangia *which are concerned in the production of seed.*

The point is of small importance practically, the important thing is the recognition of the morphological equivalent of the flower.

§ 6. **The Seed.**—The student should notice carefully that the seed is a highly specialised reproductive body consisting of structures representing three generations:—(*a*) the parent sporophyte, viz. the integument of the ovule forming the seed-coat; (*b*) the female gametophyte—the endosperm tissue; and (*c*) the new sporophyte in embryo.

§ 7. **Comparative Summary.**—In *Phanerogams*, as in Vascular Cryptogams, there is an **alternation of generations**, but it is very much less distinct. The male and female prothalli are even more reduced than in *Selaginella*. This extreme reduction of the gametophyte is characteristic of the Flowering Plants.

More important differences, however, have to be noticed. The megaspore (embryo-sac) is not set free from the sporangium (nucellus). The female prothallus is developed inside the nucellus. The other differences are correlated with this. The special process of pollination is necessary in order to bring the microspore into the neighbourhood of the megaspore, and the male cell, which, except in the case of the more primitive types of Gymnosperm (see p 449), is not a spermatozoid, but a motionless gamete, is carried to the neighbourhood of the ovum by a special organ, the pollen-tube.

Finally, there is the most characteristic difference of all—the formation of a seed. This also is clearly due to the retention of the megaspore in the ovule. It should be borne in mind, however, that the formation of a seed is not confined to the Phanerogams

CHAPTER XVIII.

RELATIONSHIP BETWEEN VASCULAR CRYPTOGAM AND FLOWERING PLANT

§ 1. **Homology based on Relationship.**—While studying the types discussed in the preceding pages the following questions have probably occurred to the mind of the student—What is the meaning of these homologies? Why should there be such resemblances in the development and life-history of plants which in many other respects differ so widely from each other? The answer to these questions is given by the **Evolution Theory,** now generally accepted by biologists in one form or another. It explains the homologies discernible amongst the plants we have been considering as due to an actual **relationship** existing between them—in other words, to the fact that they are *descended from common ancestors* To make this clear the consideration of a few important principles is necessary

§ 2 **Struggle for Existence.**—Let the student consider how numerous are the seeds produced by any one plant, and then reflect that the number of individuals in any one species remains approximately the same from one year to another. Evidently very few of the seeds develop into mature plants Some fail to reach a suitable soil, others produce seedlings which, however, are crowded out and killed by other and hardier plants—and so on. There is, evidently, a very keen *struggle for existence,* in which those which are best fitted, or most favourably circumstanced, will survive.

All organisms are subject to this struggle for existence, which is keenest between members of the same species.

§ 3 **Heredity and Variation.**—It is well known that the characters of parents are transmitted to their offspring, so that the offspring resemble their parents more or less closely This is the principle of *heredity*.

Now if the offspring were exact copies of their parents and all *equally vigorous*, it would be a matter of *chance* which of them survived in the struggle for existence; those would survive which *happened* to be most favourably situated But the offspring are not exact copies of the parents. As we know, they exhibit individual differences, some of which may appear for the first time in the history of the race These characters in which offspring differ from their parents, or from other members of the species, are called *variations*

Variation, *i e* the fact that these variations do occur, introduces a new factor into the struggle for existence Survival is not to the same extent a matter of chance Some of the variations exhibited by plants may be useful or advantageous, *i e* they may give the individuals possessing them an advantage over other individuals in the struggle for existence by enabling them to cope better with the external conditions to which they are subjected Thus in the struggle for existence the fittest will survive and their advantageous variations will tend to be transmitted and even intensified in their offspring.

§ 4 **Natural Selection—Adaptation.**—In each generation, the influence of the external conditions, by killing off the weaklings, unconsciously *selects*, as it were, those which by reason of some useful variation are more fitted for survival. This unconscious selective process, depending on the struggle for existence, is constantly operating in nature, and has been called *Natural Selection* It may be compared with the conscious selection by a gardener, for purposes of propagation, of plants showing variations which he wishes to intensify.

Thus, in the evolution of plants, new characters would arise as small useful variations preserved by natural selection and intensified in the course of generations. These characters would be suited to the environment of the plant

—in other words, they would be adaptive characters, otherwise they would not have been preserved by natural selection This, in large measure, explains the adaptation to environment which is everywhere manifested by plants.

Under changing conditions of environment, species which are incapable of appropriate adaptive variation tend to become extinct

§ 5. **Origin of Species, Genera, etc.**—If the student has followed what has been said above he should have no difficulty in realising that the forms of plants would become immensely modified during the lapse of long periods of time Within the limits of a single species several distinct **varieties** might appear After a still longer period the characters which distinguish these varieties would be intensified and would eventually be constantly transmitted The varieties would then be elevated to the dignity of **species.** In this way the original species would give rise to a group of species, *i e* a **genus.** Similarly, the genus might give rise to a group of genera, forming a natural order, and so on.

§ 6 **Homology and Analogy.**—While in the course of evolution the forms of plant members would undergo extensive adaptive modification, many of *the general developmental characters of ancestral forms, more or less modified, would be constantly transmitted. These would be recognised as homologies in their descendants.* The nearer the relationship the more numerous and complete would be the homologies. In existing plants ancestral characters often have a purely morphological value, their original biological significance having been lost On the other hand, it is because adaptive modification may *similarly* affect *different* members in different plants that we so frequently find examples of members which are *analogous*, but not homologous (see p. 18) It is evident that analogy is no indication of relationship. Aquatic plants, for example, have many features in common, but nevertheless no general relationship exists between them.

§ 7. **Causes of Variation.**—*Germinal variations* are variations due to some change or modification of the material (germ-plasm) of the germ-cells (gametes). The causes of such change are obscure; some are inclined to ascribe them to changes in the nutrition of the germ-plasm. These variations are transmissible by heredity.

On the other hand there are variations induced by the action of the environment on the body of the parent. These somatogenic variations are commonly called "acquired characters" It was formerly believed that these variations also could be transmitted, and thus afforded material for natural selection to work on. There are, however, cogent reasons for believing that this is not the case, although some hold that by the action of the environment on the germ-cells a cumulative effect may be produced in the course of a few generations.

By many these somatogenic variations are ascribed to the *direct action* of the environment, *i e.* they are believed to depend on physical and chemical changes produced by external conditions. In some cases no doubt this is true, but it is important to notice that many of these variations are adaptive, and represent definite and apparently *purposive* responses on the part of the plant to changes in its environment. It seems clear that in these cases the plant itself must be taken into account, and that its power of adaptation is an important factor in the question. This power of adaptation, or adaptability, is possessed in varying degrees by different species of plants It depends on the *specific protoplasmic constitution* of the plant, which is transmitted from parent to offspring, and which has been acquired, through natural selection, in the struggle for existence.

§ 8. **Continuous and Discontinuous Variation.**—In most cases the variations exhibited by the members of a species with regard to any particular character are minute and merge into each other so as to form a continuous series. Variations of this kind are called **fluctuations.** On the other hand variation is sometimes discontinuous, *i.e.* the variation seems to appear abruptly without any intermediate or transitional stages. Variations of this kind are called **mutations.**

Till quite recently it was generally believed that the small fluctuational variations constituted the material from which species were slowly evolved by natural selection Strong reasons have now however, been adduced for believing that the variations known as mutations are *incipient species*, and that fluctuational variations give no handle to natural selection, that at most they can give rise only to local varieties or races This view has been ably advocated by several biologists who have been prosecuting an experimental study of variation according to the principles of heredity laid down by Mendel. They regard mutations as true germinal variations, and fluctuations as being somatogenic variations induced by environment.

The question as to which view is correct can only be settled by a much more exhaustive study of the problems of heredity and variation than has yet been made Possibly a *via media* may be found In any case natural selection would still be a factor in evolution; variations, whether fluctuational or mutational, before they give rise to new species, must pass through the sieve of natural selection If, however, the mutation theory is correct, it means that evolution is a process which takes place by distinct steps instead of slowly and imperceptibly as we have hitherto believed.

§ 9. **Course of Evolution in the Higher Plants.**—We may suppose that the common ancestors of the Vascular Cryptogams and Phanerogams were plants showing a distinct alternation of generations—the sporophyte differentiated into root, stem, and leaf, and producing asexual spores—the gametophyte a green thallus, bearing both antheridia and archegonia Some of the ancestral characters have been inherited in common by the descendants These constitute the homologies we have recognised. The differences or modifications have arisen as different adaptations to changing conditions of environment Let us see if we can trace some of the more important of these.

We must first ask the student to notice that the sporophyte is evidently a plant adapted to aerial conditions, while the gametophyte, as we find it in the Fern or *Equisetum*, and, presumably, as it existed in the ancestral forms, is adapted to moist conditions Further, that in the Flowering Plants we have plants *completely* adapted to aerial conditions *

On the view that cross-fertilisation is of advantage to plants, we can understand the gradual evolution of unisexual prothalli (e g *Equisetum*) But why the reduction of prothalli and the heterosporous condition? This is probably traceable to the more complete adaptation of the plant to aerial conditions Evidently, if there was any uncertainty as to the conditions being sufficiently

* Aquatic Angiosperms have *returned* to aquatic conditions Their ancestors were aerial types—cf the whale among air-breathing vertebrates

moist for the development of well-formed prothalli, the storing up of food-material inside the spore would be a useful variation It was more necessary in the case of the female gametophyte because it had to nourish the embryo—hence the differentiation of a megaspore. From this stage onwards the spores and prothalli may be regarded simply as organs having for their function the production of a new sporophyte

Considering the uncertainty of the microspores reaching the megaspores the advantage of the retention of the megaspore in a secure and definite position in the sporangium will be perceived. The microspores being small would be readily blown about by the wind, and we can imagine that there were special means for catching them (cf secretion of mucilage from the micropyle of *Pinus*). Here we trace the beginning of pollination

At first, probably, the microspore germinated on the surface of the female prothallus, and the spermatozoid made its way to the archegonium in water present on the surface of the prothallus and probably in part excreted by it We can understand the gradual enclosure of the megaspore on the view that the embryo would be better protected and have a better chance of surviving The development of a pollen-tube, which is correlated with this, would probably be stimulated by the presence of water on the surface of the partly covered megaspore or prothallus

The study of fossils indicates that in primitive seed-plants fertilisation was effected as in living Cycads (p 398) The dependence of fertilisation on the presence of water was obviated finally by the pollen-tube itself carrying the male cell to the oosphere

In Gymnosperms we have clear evidence that a number of distinct megaspores and embryos (polyembryony, p 391) were present in primitive seeds. The advantage of the reduction to one is evident, for one strong and well-nourished seedling is much more likely to survive than two weakly ones After the complete enclosure of the megaspore, it lost its cuticularised coat, which is still found in Cycads, and the archegonium, being now a useless

organ, gradually disappeared, the oosphere or ovum only persisting. Finally, the late development of endosperm in Angiosperms is of distinct advantage, as it is not required if fertilisation is not effected.

Much of this, of course, is hypothetical, but close study of living and of fossil types affords evidence that it represents approximately the general course of evolution in the higher plants

§ 10. **Origin of the Flowering Plants.**—The origin of the Dicotyledons, which appeared towards the close of Mesozoic times and rapidly attained a dominant position, has till recently been a mystery There is now reason to believe that their ancestors are to be found amongst the Cycad-like plants (Cycadophyta) which flourished so abundantly in Mesozoic times. In the most important group of Cycadophyta, the Bennettiteæ, the flowers (cones) were hermaphrodite. They consisted of an axis bearing stamens below and ovules above, together with intervening scales which also formed a sort of perianth below the stamens. The resemblance of this arrangement to that of a typical dicotyledonous flower is obvious. To this has to be added the fact that the seeds were almost exalbuminous and contained an embryo with two cotyledons.

The Monocotyledons appeared about the same time as the Dicotyledons. Their origin is still obscure, but it seems probable that they represent an offshoot from the primitive dicotyledonous stock.

The Cycadophyta, from which apparently the Angiosperms (and possibly also the Gnetaceæ) have been evolved, appear to have sprung from fern-like ancestors which flourished in earlier Palaeozoic times. A group of Palaeozoic plants, the Cycadofilices, presenting resemblances to both Ferns and Cycads has for some time been recognised. Recently it has been found that these fern-like plants produced seeds resembling in important respects those of Cycads For this reason the plants are now called Pteridospermeæ

The origin of the Conifers is still doubtful. They appeared in Palaeozoic times and were allied to an extinct

group of Palaeozoic Gymnosperms, the Cordaiteæ, which show affinities with the Cycads. Thus they may represent an earlier offshoot from primitive Pteridospermeæ.

§ 11 **Evolution of the Flower.**—If the views as to the relationship between Dicotyledons and the Bennettiteæ are well founded we may conceive the primitive Angiospermous flower as being hermaphrodite and consisting of an elongated axis bearing stamens below and carpels above. There can be no doubt it was anemophilous. The highly specialised Angiospermous flowers have been derived from this primitive type Some of the growth processes which have led to modification of floral structure have been mentioned on p. 244. We have now to consider these modifications from the standpoint of evolution and to recognise their biological significance.

If we remember that the course of evolution has been in the direction of the more perfect adaptation of the flower to the function of seed- and fruit-production, we shall understand that the evolutionary history of the flower may be interpreted by reference to the more important adaptations that have taken place It is well to remember, however, that specialisation, or advance in organisation, has followed many lines, and that along particular lines it may be illustrated within the limits even of a single order Our natural orders cannot be arranged in a linear series, but are best regarded as the terminal twigs of branches given off along the main stem of Angiospermous development.

(1) *Protective adaptations.*—The fundamental distinction between Angiosperms and Gymnosperms, the formation of a pistil, no doubt arose as an adaptation securing the better protection of ovule and seed The close association of leaves or bracts under the sporophylls was probably the precursor of a protective perianth. Here also we must refer to the gradual abbreviation of the floral axis, and the transition from hypogyny to perigyny and finally to epigyny. This marks an advance in organisation: the ovary and seeds were better protected by being enclosed in the thalamus.

(2) *Adaptations for more economical and efficient seed-production*.—At first the pistil was probably apocarpous, with few ovules in each ovary. Ready pollination would be facilitated by increase in the number of ovules or their aggregation in a single compound ovary. This explains the evolution of the syncarpous pistil. As pollination became more certain there would be a reduction in the number of stamens and carpels. This is characteristic of the higher and more specialised orders (*e g* amongst the Sympetalæ). Amongst the Compositæ the ovules are reduced to one in each ovary. Specialisation here has followed the line of elaboration not of the single flower, but of the inflorescence of small flowers

(3) *Adaptations for insect-pollination*.—The evolution of Angiospermous flowers is intimately connected with insect-visitation and cannot be followed with any clearness except by reference to it. The transition from wind-pollination to insect-pollination and the general occurrence of the latter* are, of course, explained by the fact that insect-pollination is more economical and more certain

At first insects probably visited flowers to feed on the pollen A slight secretion of sweet substance by the floral leaves, serving as a further attraction, no doubt led to the evolution of **nectar-glands**, while the sterilisation of the outer series of stamens probably led to the evolution of the **corolla**, and slight variations in form, facilitating the movements of insects, to the evolution of **mechanical contrivances.**

At first, no doubt, the flowers were open, and the honey freely exposed. Adaptation to pollination by longer-tongued insects, necessitating concealment of honey, explains the evolution of the tubular form found in many flowers This tubular form has arisen in various ways amongst the Archichlamydeæ, in the Sympetalæ it is secured by the gamopetalous corolla, whose evolution is thus explained. The epipetalous condition of the stamens, which is usually associated with the gamopetalous corolla, allows for the further narrowing of the tube

* Some writers deny that any existing Angiosperm is *primitively* anemophilous.

§ 12. **Fruits and Seeds.**—Similarly we can explain through natural selection in the struggle for existence the evolution of succulent and other forms of fruit, and of the various contrivances and mechanisms for the dispersal of seeds and fruits.

CHAPTER XIX.

THE ECOLOGY OF PLANTS.

§ 1 **Plant Ecology** is the study of the relation of plants to their environment. Evidently it is a study which implies a more or less intimate knowledge of both the structure and the physiology of plants, and some acquaintance also with the facts and principles of Plant Evolution Some reference to the subject has already been made in Chapter VIII , it will now be considered in greater detail.

§ 2 **Adaptation.**—We have seen that amongst plants there is a constant struggle for existence, which is keenest between allied plants having similar habits and requirements. The successful ones are those which secure an advantage owing to more perfect adaptation Some may become better adapted to the conditions of temperature; others to variations in the amount of moisture present at different periods Others, again, may maintain their position because they possess a ready and effective method of seed-dispersal. At the same time it must be remembered that what counts in the struggle for existence is the whole equipment of the plant, not the possession of any single adaptive or advantageous feature

In all cases where the struggle is severe the weakest and worst equipped are driven to the wall. Such unsuccessful competitors may die off and become extinct, but, frequently, plants that fail in open competition are able to exist in special localities, where there is less competition, owing to their having acquired some special adaptation Some, for example, may be able to grow in sandy places near the sea where the soil-water contains a large amount of salt; others may become adapted to live in marshy places, or in conditions which are completely aquatic.

Occasionally unsuccessful types develop the climbing habit, or become epiphytic or parasitic upon their stronger neighbours, and thus succeed in maintaining themselves

All these different "types" of flowering plant, which are characterised by adaptation to special conditions of existence, have been derived from typical land-forms. It has to be noticed, in this connection, that specialisation usually entails a loss of adaptability, *i e* a loss on the part of the plant of the power of accommodating itself to new surroundings. Hence highly specialised plants must usually conquer their surroundings in order to survive, and remain as "fixed" types as long as they can do this, but become extinct when subjected to adverse conditions.

§ 3 **Environment.**—All the factors of the environment must be taken into account These factors fall into four main groups · (1) the **physiographic factors,** including altitude, exposure, slope; (2) the **climatic factors,** including temperature, rainfall, light, (3) the **edaphic factors,** including the physical and chemical characters of the substratum, *i e* in most cases the soil, (4) the **biological factors,** including other plants, animals, and **man.**

The external conditions of environment vary widely in different localities and in different parts of the globe. It is important, therefore, to consider the influence they exert on the distribution of plants.

§ 4. **Temperature.**—So far as can be observed no striking structural modifications are associated with differences in temperature Ability to withstand extremes of heat or cold appears to be a specific property of the protoplasm and is not provided for by any visible structural adaptations

Temperature, however, is of the utmost importance in relation to all the vital processes, and also exerts a profound influence on the geographical distribution of plants in correlation with the fact that the average temperature and the range of temperature both vary widely in different parts of the globe and also in different localities.

On the whole, most plants prefer temperatures lying between 20° and 30° C, although many are specialised to withstand very high or very low temperatures.

§ 5. **Moisture.**—So far as structural modification is concerned water is undoubtedly the most important factor of the environment The whole organisation of a plant, internal as well as external, bears a close relation to the conditions under which water has to be absorbed, distributed, and, in many cases, economised. This will be clearly brought out in connection with the various biological groups of plants (§§ 9-25)

Water exerts an important influence not only on the local or topographical distribution of plants, but also, second only to that of temperature, on their wider or geographical distribution Within the Tropics there are certain parts where the wet season continues almost without intermission during the entire year, although in most parts dry and wet seasons alternate in regular succession A large part of the warm Temperate Zone lying north and south of the Tropics is subject to drought or has only periodical rainfalls. In the Temperate Zone there are variable winds and rain These three regions are characterised by plants which differ as regards the amount of moisture they require (hygrophytes, xerophytes, mesophytes respectively—see § 9).

§ 6 **Light.**—We can frequently recognise structural modifications developed in response to the influence of light. Shade-plants have frequently large leaves and long internodes, and the palisade tissue of the leaves is poorly developed Sun-plants, on the other hand, more especially if exposed to very intense light, have small leaves and short internodes, owing to the retarding action of light on growth, and the palisade tissue is well developed It is partly for this reason that alpine plants have a more condensed habit than plants growing in the valleys Possibly also the forms assumed by leaves are largely due to the influence of light

Light determines mainly very local distribution, al-

though many of the distinguishing characters of plants in widely separate regions (*e g.* Tropical and Arctic plants) are correlated with variations in the intensity and duration of the light to which they are exposed Some plants love the shade, others full exposure to the sun. A certain amount of the light rays are absorbed in passing through water. Hence sea-weeds and fresh-water plants cannot exist below a certain depth, because insufficient light would reach them Plants with thick fleshy leaves or cladodes prefer bright sunlight because otherwise the inner assimilating layers only receive very weak light. The Wood-sorrel (*Oxalis acetosella*), Sweet Violet, Wood Geranium, and most Liverworts, Mosses and Ferns are good examples of shade-loving plants The Stone-crop (*Sedum*), the House-leek (*Sempervivum*), Sun Spurge (*Euphorbia helioscopia*), Sunflowers, Field Poppies, and most Cactaceæ are examples of sun-plants.

§ 7 **Wind.**—The characteristic appearance of bushes growing along exposed ridges (sea-cliffs, etc.), where the branches bend over in the direction of the prevailing winds, is partly a mechanical effect of the wind, partly due to the death, by excessive transpiration, of those parts of the plants directly facing the wind The excessive transpiration produced has a desiccating effect on vegetation, best seen of course in the case of shrubs and trees This accounts, in part, for the dwarfed and stunted form assumed by plants growing in exposed regions at high elevations, and, in combination with the destructive action of wind, explains why the conditions in such regions are unfavourable for the growth of trees.

§ 8. **The Soil** *or substratum.*—In considering the influence of the soil on plants attention must be given to both its physical and chemical properties. With regard to the physical properties the most important are porosity, capillarity, and water capacity.

Certain modifications are apparently to be ascribed to the chemical properties of the substances present. Thus plants grown in soils rich in chalk or clay differ in certain

respects from plants grown in soils deficient in those substances. In a few special cases marked modifications seem to have been produced in this way

On the other hand many modifications are due not to the chemical properties of the substances present, but to the fact that they alter the conditions with regard to the absorption of water The presence in large amount of soluble salts in the soil, for example, renders the absorption of water difficult, and leads to xerophytic adaptation According to some, however, the storage of water in such cases is an adaptation, not so much against "physiological drought" as to diminish the injurious and poisonous effects of undue concentration of the absorbed substances in the plant cells.

The substratum, taking the term in the widest possible sense, determines very local distribution. Many plants grow only in bogs or swamps, others in peaty soils or in soils rich in vegetable remains, others again in or on running or stagnant water, others on sandy or muddy coasts.

Similarly, some plants prefer chalky soils, others rich loam, while some succeed in maintaining themselves on the poor thin soil derived from granite rocks In these cases, however, the relation to soil is not definite Thus a plant which in one region is restricted to a chalky or siliceous soil may in another region be found growing indiscriminately on different soils In explanation of this we have to remember that various other factors have to be considered—*e.g* the physical properties of the soil, the presence or absence of other kinds of plant-food Another important factor is the amount of competition to which a plant is subject, a plant may inhabit a poor soil, not from choice, but from necessity

The physical properties of the soil are apparently much more important than the chemical in determining the distribution of plants.

§ 9. **Plant Associations.**—From what has been said it will be recognised that various plants (belonging to widely different orders) grow together in certain localities evidently because they like (that is, are adapted to) the

same kind of soil, the same conditions of dryness or wetness, the same amount of light or shade, etc. Such biological groups of plants (Marsh-plants, Shore-plants, Climbing-plants, etc.) may be called **Plant Associations.**

From the ecological point of view Flowering Plants may, first of all, be divided into three main groups or categories —(*a*) **Geophytes**, (*b*) **Aerophytes** or *Epiphytes*, (*c*) **Hydrophytes.** Geophytes are land-plants fixed in the soil by means of roots. Aerophytes or epiphytes (see p. 484) are land-plants which grow attached to other plants. Hydrophytes are aquatic or water-plants; they are said to be *hydrophilous* (*i.e.* water-loving) and are subject only to aquatic conditions. In addition to these there are the small groups of parasitic and saprophytic flowering plants whose characters have already been considered (p. 196).

Amongst geophytes, which include the vast majority of Flowering Plants, various groups or types of adaptation are distinguished. Plants which grow in very moist conditions, in marshes or swampy ground, on river-banks or on ditch-sides, and which therefore come nearest to being aquatic, are called *hygrophilous* (moisture-loving) plants or **Hygrophytes.** They are usually of large size and luxuriant growth, devoid of thorns (though prickles may be present), and with an abundance of stomata and a thin cuticle. The root system is not strongly developed, and the leaves have frequently elongated apices ("drip-tips") for throwing off water. Most Ferns, and Palms, Bananas, etc., are hygrophilous.

At the other extreme are *xerophilous* ("drought-loving") plants or **Xerophytes** (see p. 217). Cactuses are typical xerophytes, and so also are very many Acacias and Euphorbias.

Between xerophytes and hygrophytes we find a great many intermediate forms (**Mesophytes**), which grow in meadows, pastures, cultivated fields, and in woods and plantations of deciduous trees (Beech, Oak, Birch, etc.). These plants show no decided xerophilous or hygrophilous characters, though some approach xerophytes in form and structure and others approach hygrophytes.

Woody perennials (trees and shrubs) with deciduous leaves show distinctly xerophilous characters in winter (the protected winter-buds, cork-covering of stems and of leaf-scars, cork-layer closing up the lenticels), while in summer they bear thin leaves like those of mesophytes or hygrophytes It has been proposed to call such plants, which are more or less hygrophilous in summer and xerophilous in winter, **Tropophytes** (*i e.* "changing plants") This applies only to deciduous plants; evergreen land-plants are more or less strongly xerophilous in character.

It must be remembered that no hard-and-fast lines can be drawn between these types Some aquatic plants can, when the stream or pond dries up, continue to live and grow, sometimes even more vigorously, in the air, thus changing from hydrophytes to mesophytes The same species of plant may be found growing under hygrophilous or xerophilous conditions in different localities In each case the structure of stem and leaf, as well as the form of the leaves and the general habit of the plant, become modified to suit these different modes of life.

§ 10 **Duration and Seed-Production.**—Plants may be classified into annuals, biennials, and perennials, according to whether their life-cycle is completed within one, two, or several years Again, plants are either **monocarpic** and completely exhaust themselves the first time they produce seed, or are **polycarpic** and spread their production of seeds over several seasons. Hence of necessity annuals and biennials are monocarpic, whereas perennials may be either polycarpic or monocarpic

Only a few perennials are monocarpic They may either be arboreal (many Palms and Giant Bamboo) or herbaceous, as in the slowly growing Century Plant (*Agave*) Such plants vegetate, grow, and store up food materials often for more than twenty or thirty years, at the end of which time they produce a great crop of fruit and seeds and die exhausted.

Biennials devote their first season to accumulating food, which is stored in the root (Carrot, Parsnip, Beetroot) or in the hypocotyl (Turnip, Radish) After perennating through the winter, they utilise their surplus food in producing a large number of flowers and fertile seeds, and then die If exhaustion is prevented by cutting off the fruits before they grow, life may be prolonged almost indefinitely.

In some annual plants termed *ephemerals*, the duration of the life-cycle is so shortened as to enable several generations to follow one another during a single season, only a few weeks intervening between the germination and fruiting of each individual (Shepherd's Purse, Chickweed, Groundsel). The Groundsel in fact grows and fruits all the year round There is, however, no sharp distinction between annuals and "ephemerals"

Both the duration of a plant and the number of times it may flower are liable to be modified by external circumstances. Many annuals may become biennials if a wet summer or rich soil retards flowering, and if the winter frosts are not so severe as to kill them. Starved annuals may become ephemerals by shortening their life-cycle Such plants as the Castor Oil and Scarlet Runner are perennials in warm climates, but become annuals in cold ones, since they are killed by the winter frosts, whereas their seeds survive

§ 11. **Effect of Changing Seasons.**—We have seen that water-supply and temperature are two of the conditions on which normal protoplasmic life depends These vary enormously with (*a*) climate, (*b*) seasonal changes The simple life-cycle thus becomes *greatly complicated* in correlation with these two factors, and in all parts of the world, except certain regions of the moist Tropics, the influence of the rhythmic alternation of the seasons is deeply felt This influence of annually changing seasons is generally felt in the form of *one season being unfavourable for growth*

The various modes by means of which plants manage to persist in a more or less *dormant* condition over unfavourable seasons are included under the term **perennation.**

Winter Perennation.—In adaptation to their surroundings the plants of cold climates have acquired various means of surviving the cold period of the year Except in the case of evergreens, which retain their leaves for two or more years, the leaves usually die and fall off at the onset of winter This resting condition is induced not so much by the direct action of the low temperature as by the deficiency of water consequent on the reduction of root-absorption which it causes. It is the same danger of desiccation during winter which has caused the leaves of evergreens to become leathery, or to acquire thick cuticles

The stems and branches of shrubs and trees are more exposed to extremes of temperature than the roots They are able to withstand severe cold owing to the cork layer which covers them.

mainly because it protects them against the loss of water, and to a less extent because it acts as an insulating jacket, keeping in heat just as a blanket would do

Drought Perennation.—In tropical climates the seasons are determined not so much by the temperature as by the amount of rainfall. Typically one or two wet and dry seasons occur each year in alternate succession, and if the dry season is at all prolonged, the vegetation suffers a pronounced check. The special adaptations by which plants are enabled to survive periods of drought in warm climates are often very similar to those exhibited by the plants of cold climates. Thus in both cases protection may be afforded by the loss of leaves, which obviates undue transpiration, or by the possession of the evergreen habit (persistent leathery leaves with thick cuticle and water-storing devices)

§ 12. **The Modes of Perennation** may be summarised as follows —

1 *The Evergreen Tree.*—The *foliage persists,* but is *protected*

2. *The Deciduous Tree* —The foliage is shed for *winter-cold* or *summer-drought*. The *shoot* is protected by its cork jacket, and the growing-points perennate as *buds* covered by protective scales, or hair.

3 *Herbaceous Perennials.*

(i) Only the flowering shoot dies, as in summer-flowerers such as Buttercups

(ii) *All the aerial portions die,* as in most plants with rhizomic stems.

4 *Special Types of Subterranean Perennation*

(*a*) *The Bulb.* (*b*) *The Corm* (*c*) *The Rhizome.*	The Bulb and Corm may be regarded as perennating buds, while the Rhizome is a stem which has gone below ground for protection

5. *Seed Perennation.*—This is the most perfect type of perennation known, for the dried dormant plantlet provided with food-materials and enclosed in its protective coverings retains its vitality often for many years and under most adverse circumstances.

§ 13. **Plant Societies.**—We shall now proceed to consider in detail the features presented by some of the more important biological groups of plants, and of plants growing in special regions.

§ 14 **Water-Plants** are subject to less extremes of temperature than land-plants, for the water in which they grow takes longer to be heated and longer to cool Owing to this greater uniformity of conditions many of them are very widely distributed Being more or less screened by the water from the action of light they show many of the characters of shade-loving plants (long internodes, no palisade tissue, presence of chloroplasts in the epidermal cells). The structural modifications of aquatics have already been considered in Chapter VIII (p 216).

In plants growing in running water, such as spp of *Potamogeton*, the leaves are usually long and ribbon-like, the form best adapted to resist the movement of the water. In still water the leaves are usually much divided, as in *Utricularia*, *Trapa*, Water Buttercups, and Water Milfoil, and thus present a larger assimilating surface to the water.

Leaves which float on the surface of the water are usually entire and rounded or slightly lobed, as in the Lotus (*Nelumbium*), Water-lilies (*Nuphar*), some species of *Potamogeton*, and Duckweed (*Lemna*), and bear stomata on their upper surface, which is covered with cuticle or wax so as to prevent wetting These floating leaves have the same structure as those of land-plants, but the air spaces are very large and are continuous with air-passages running down the leaf-stalk to the submerged stem and roots, as in *Nelumbium* In submerged parts these air-spaces not only enable the plant to float upright, but they also convey air to the lower parts growing in deep water or in mud, where little or no oxygen is present for respiration In many water-plants with floating leaves the petioles are partly or wholly converted into large bulb-like floats containing air (e g *Trapa*, the Singhárá plant).

Carbon dioxide dissolves readily in water, and therefore the percentage of this gas in water is higher than in air. Since a submerged plant gets water, salts, carbon dioxide,

and oxygen so easily, and lives in very favourable conditions generally, it grows rapidly, branches freely, and reproduces itself largely by vegetative means, chiefly by the decay of the older parts setting the branches free, or by branches breaking off.

The majority of water-plants are perennial. The water-plants of tropical regions grow continuously all the year round, not being hampered by either a cold or a dry season. In temperate regions growth is interrupted by the winter, and various methods of perennation occur. In some cases—e g *Callitriche*—the plant remains unaltered, merely sinking to the bottom, in Water-lilies food is stored up in the rhizome; in Arrow-head (*Sagittaria*) tubers are formed. A very common mode of perennation is the formation of winter-buds, which are developed at the ends of the branches These buds are large, their leaves contain reserve food; they drop off and remain at the bottom during the winter, growing up in the spring Winter-buds of this kind occur in Water Milfoil, Water Violet, Bladderwort, and various species of *Potamogeton*.

Since water-plants reproduce themselves so extensively by vegetative methods, it is not surprising that they usually flower much less freely than land-plants In a few cases the flowers are adapted for pollination by the agency of water—at the surface (*Vallisneria*) or below it In most water-plants, however, the flowers are formed above the water, and are adapted for pollination by wind or by insects. In the former case much of the pollen must fall into the water and be wasted; in the latter, the scarcity of insects makes the chance of cross-pollination small.

The plants so far mentioned grow with the entire shoot under water (except the flowering branches) and the leaves submerged or floating In some Water Buttercups and in *Trapa* part of the shoot remains below and bears divided leaves, while part grows upwards and bears broad, floating, or aerial leaves. Some plants—e g. *Polygonum amphibium*—can grow either submerged or on muddy soil with their shoots in the air In such amphibious plants the leaves of the land form are broader, and the stem-

and leaf-structure resembles that found in ordinary land-plants.

In the case of many water-plants it is found that they can be grown on land, either by transplanting them to ordinary soil or by sowing the seeds in soil In the former case the new shoots formed differ from the water-form in regard to leaf-shape and the leaf- and stem-structure; in the latter case the seedlings produce at first some leaves of the aquatic type, and later bear broad land-leaves. In some cases the change from land-plant to water-plant can be brought about, especially with plants which grow ordinarily in damp places

§ 15 **Marsh Plants.**—Under this heading we include those plants whose roots and rhizomes, or shoot-bases, are in water or mud, while their leaves, or foliage-bearing shoots, and of course the flowers, grow in the air. Between typical aquatics, marsh-plants, moisture-loving plants, and land-plants there is every stage of transition. We may, however, distinguish between associations of permanently submerged water-plants and those characteristic of marshes and bogs in which the substratum alternates between long periods of wetness and shorter periods of more or less complete drying-up The characteristic feature of marsh and bog plants is that their lower parts, buried in the mud, are adapted to aquatic life, while their upper parts, exposed to the air, either resemble those of land-plants or are adapted to withstand drought

The reduced leaf-surface and thick cuticle of Rushes, Sedges, Horsetails, etc, have often been attributed to the existence in stagnant mud, especially in peat-bogs, of acids produced by the decaying organic matter, this acidity making it difficult for the roots to absorb water and necessitating a reduction in the transpiring surface of the plant, But actual analyses show that in some cases at any rate the pond-mud in which Rushes and Sedges grow contains no acids or only traces of acidity, and moreover the presence of acids, in certain quantities, actually increases the rate of water absorption by plants.

In order to meet these objections it has been suggested

that these "marsh xerophytes" owe their mixed characters to the persistence of ancestral features in spite of a striking change of habitat, and that they are now "hydrophytes wearing a xerophytic mask." Perhaps the bad aeration of the roots, which usually show marked hydrophytic characters, especially in the existence of abundant air-spaces, has something to do with the xerophytic structure of the shoot in both bog and marsh plants, and the "physiological drought" theory (i e. the view that the acidity of the substratum prevents absorption and acts in the same way as actual lack of water) may hold good for bog plants At any rate, the biology of marsh and bog plants appears to be somewhat complex.

In the plains of India, owing to the well-marked distribution of the year into a dry season of considerable duration and a wet season which is comparatively short, bog and marsh plants are rare During the fierce heats of the dry season, everything resembling a marsh is liable to become dried up at a very early period, and only in very few places do such stations for plants remain marshy throughout the year

What species there are belonging to this category are mainly to be found in the hills, where the country does not dry up to so great an extent in the dry season, and there, especially in the north, may be found many of the same genera as in Europe, but in the plains there are but few plants to be seen that belong to this group These include a good many of the Sedge Family, especially *Carex*, *Cyperus*, *Eleocharis*, *Scirpus*, *Fimbristylis*, and others, a few Grasses, Rushes (*Juncus*), and others In the rice fields there grows a special flora of small annuals which die when the fields are drained for the harvest, but these are as much water-plants as bog-plants.

§ 16. **Moorland Vegetation.**—The greater part of India, being flat, contains nothing in the nature of moors, which are elevated portions of land covered with a peaty soil, and inhabited by various xerophytic plants. But in the hills, and more especially in the Khasias and the Nilgiris, such tracts of land may be found—open rolling expanses of grass land, sometimes boggy in the hollows near the streams. The flora of the corresponding vegetation of the Ceylon mountains has been very thoroughly worked out, and it will be best to use that as an illus-

tration, which will apply to others of these areas in India

The soil at high levels is very rich in humus, and is of an extremely fine consistency, the chief vegetation upon it is grasses, which at the lower levels usually grow in a very tufted manner, but at the highest elevations form a turf. In the swampy places more especially, species of Cyperaceæ and many Eriocaulons form the bulk of the vegetation, though they are also common on the more open and drier places Trees, on the other hand, are comparatively rare, in Ceylon *Rhododendron arboreum* being the only one at high levels, *Careya arborea* the only one at moderate elevations At high levels the flora changes type as compared with that at the lower elevations, becoming much more like the European flora in its composition, including many species of such genera as *Anemone*, *Thalictrum*, *Ranunculus*, *Berberis*, *Hypericum*, *Rubus*, *Potentilla*, *Alchemilla*, *Agrimonia*, *Valeriana*, *Dipsacus*, *Campanula*, *Gentiana*, and many others; while among the chief ornaments of the grass lands are such flowers as those of *Exacum*, *Satyrium*, and others.

Bearing in mind the fact that the soil on which these plants live is one which does not retain water well, and that for a few months of the year, at any rate, they are exposed to severe drought, one will expect that many of them should exhibit xerophytic characters, and is only surprised to find to what a small extent these characters are shown A good many exhibit rolling up of the leaf, though not in its most pronounced form. Others with thin needle-like leaves are very common, yet others have small leaves closely crowded together. In others again protection is obtained by means of a coating of hairs, of greater or less density, upon the surface of the leaf Some have a coloured pigment in the leaves, and especially in the young leaves Some have the leaves in a hanging position or otherwise so arranged as to present a sloping or vertical surface to the rays of the sun Sleep movements of the leaf are very common, and there are other methods for reducing transpiration, but, as already mentioned, the amount of reduction is by no means so large

as might be expected, and the plants do not at first sight look very xerophytic.

A remarkable fact with reference to these high level moors, in Ceylon at any rate, is that they do not occupy the highest points of the hills or ridges, and the forest the valleys, as one would naturally expect, but the reverse, the forest being upon the ridges, and the moors occupying the valleys, grassy if the valley be dry, sedgy if the valley be wet. The boundary between the moor and the forest is marked off with extraordinary sharpness, and remains very constant from year to year. A few strides carry one from the moor into the forest, which has a totally different vegetation, whilst along the edge of the forest there is a special vegetation, which has a character distinct from either, including large quantities of *Rhodomyrtus tomentosa* and other species which are rarely found growing in either forest or moor.

§ 17. **Bog Plants.**—The typical bog occurs upon moors, and is consequently not common in India. Its vegetation consists of peat-forming and peat-loving plants The distinctions between a marsh and a bog are fairly clear in most cases, though it is needless to remark that transitions from one to the other are not infrequently to be found The typical marsh occurs on low-lying ground, its water is rich in mineral substances, especially in lime, and its plants grow rapidly, producing numerous leaves and branches each year, and may become either tall or short, whereas in a typical bog the plants are most often short, the water is poor in lime and in other salts, and the plants in general grow but slowly.

The peaty soil in which bog-plants grow is not sufficiently aerated for the proper formation of nitrates, so that although such soils often appear on analysis as though they should be extremely fertile, very little of the material they contain is directly available to serve as plant food. This fact perhaps largely accounts for the presence of the insectivorous Droseras in such quantity in bogs. It also helps to explain why so many of the moor plants have a mycorhiza upon their roots, and are thus able to

make use of the peaty materials by being partial saprophytes.

Bog-plants have usually more or less well-developed xerophilous characters, due largely to the excess of peaty acid, which makes water absorption difficult. Mosses, especially the bog-mosses (*Sphagnum*), play an important part in the formation of bogs, they are specially adapted for storing water. The leaf consists of a single layer of cells, which are of two kinds (1) large empty water-storing cells with pores on the walls, (2) small green assimilating cells. Each plant branches and grows upwards, while the lower parts die and lose their green colour, but are preserved from decay by the absence of oxygen and the presence of the peaty acids. In this way great masses of peat are formed

§ 18. **Humus Plants.**—Some of these simply prefer the humus as a medium on which to grow, as for example the most of the Rhododendrons which are so common in the hills Others, however, are saprophytes, and use the humus as a source of food, being aided in this by the presence upon their roots of symbiotic fungi (mycorhiza), which play the part of root hairs, and, after decomposing the humus, hand over all or part of it in a form suitable to the plant. Such plants commonly have their foliage leaves reduced to mere scales, which are not green, as in the saprophytic orchids

§ 19 **Sand-Plants.**—These include (*a*) those plants which merely prefer a sandy soil, and (*b*) those of the sea coast (**strand-plants**), which have adapted themselves to the presence of salt. Many such plants grow equally well in ordinary soil, but lose certain of their characteristics, and probably would not survive if left open to free competition. Nearly all such plants have strongly xerophilous characters; for example, reduced leaf-surface, thick fleshy or prickly leaves and stems, stunted habit, thick cuticle, deeply sunk stomata, etc.

§ 20. **Strand-Plants.**—The plants belonging to this group have been well studied in the Tropics, where they

differ comparatively little from one country to another, owing to the fact that they are often distributed by floating as seeds over great distances of ocean. They may be divided into several different associations, of which the chief are the mangroves, the beach-jungle, and the sand-plants, while there are other more special and local associations, such as that characterised by the stemless Nipa Palm, which may be well seen in parts of the Sunderbuns.

The **mangroves** grow upon the muddy swampy estuaries of the tidal rivers, where, though the tide rises and falls, they are not subject to the direct action of the waves They grow as a rule only in places where the mud is left actually bare during a portion of the day Although the plants comprised in the general term mangroves belong to several different families, they present many points of similarity, which may be regarded as adaptations to their mode of life; most of them are very much isolated in their systematic position, and the group would consequently appear to be a very old association.

The chief genus belonging to it is *Rhizophora*, the Mangrove par excellence, of which there are two or three species, other common ones are *Bruguiera*, also belonging to Rhizophoraceæ, *Avicennia* (Verbenaceæ), *Aegiceras* (Myrsinaceæ), and *Sonneratia* (Blattiaceæ). The habit of the tree or shrub mangroves is in general much the same, they grow to a moderate height only, and develop large numbers of aerial adventitious roots, both "flying buttress" roots from the main stem and supporting roots from the branches, so that a mangrove swamp is a bewildering tangle of roots. Not only are there these roots growing downwards, but in *Sonneratia*, *Avicennia*, and *Bruguiera* there are peculiar aerating roots which rise out of the mud like a crop all round the plant. These roots are formed as branches upon the subterranean roots, are negatively geotropic, and show a great development of *ærenchyma* or aerating tissue formed by the phellogen, not unlike the interior tissue of a leaf, they appear to be useful for respiration as the mud is very poor in oxygen, and are sometimes termed **pneumatophores.**

The mangroves are of necessity, like other shore plants living where the soil contains much salt, xerophytic in their structure, with thick leathery leaves, thick cuticle, water-storing tissue in the leaves, and other features .

A very characteristic feature of many mangroves is what is often called their **viviparous germination.** The seeds instead of falling into the water, where their chance of reaching a suitable spot without being altogether carried away would be small, germinate within the fruit, and produce a long stout radicle, which hangs down to a length of a foot. Finally the seedling drops, and may at once stick into the mud if the tide be low, but if the water be high it floats with the radicle downwards, and stands a chance of catching in a suitable crack as the water level falls.

The **beach-jungle** stands a little way back from the sandy shore, but is a very characteristic formation upon tropical beaches, and is composed of low scrubby trees and shrubs, including several species of *Pandanus*, the Screw-pine, trees with large flying buttress roots, and sword-like leaves arranged in 1/3 phyllotaxy, with the stem often spirally twisted, whence the name, *Pemphis acidula*, common on beaches that are washing away, *Scævola, Sophora, Thespesia*, and many others All these again show xerophytic characters of a more or less pronounced kind.

On the actual sandy beach there grows another association of plants, including many species, several of which have very striking characters. *Ipomœa biloba*, the Shore Convolvulus, has pretty purple flowers, and has long stems which creep over the sand and take root at the nodes, so that the plant will rapidly grow over and more or less bind together quite a large area of sand . *Spinifex squarrosus*, a large harsh grass, produces single-flowered spikelets with long spiny bracts, and massed together into a head, which breaks off when the fruits are ripe, and rolls along the beach before the wind until it finally breaks up and sows the seeds. *Launæa pinnatifida*, a little creeping Composite, rooting at the nodes, is very common, and there are many other plants of similar habit.

The plants of the seashore have very often fruits or

seeds which can be floated for long distances without injurious effects from the salt water The coconut (*Cocos nucifera*) has not only a thick shell (endocarp), but also a fibrous outer coating, which enables it to float long distances uninjured, and has caused it to become one of the first colonists of new land (*e g.* new coral reefs) in any part of the tropics, to such an extent that its original home is still a matter of dispute, though perhaps it most probably originated in the South Sea Islands. *Pandanus*, and many other plants of the beach, similarly have fibrous pericarps.

§ 21. **Epiphytes and Climbing Plants.**—The characters of these groups have already been considered (pp 83, 209, 217). Frequently ordinary flowering plants, possessing more or less well-marked xerophytic characters and a ready method of seed-dispersal by wind or by birds, are found growing on trees in places where humus or soil of some kind accumulates. True epiphytes may be distinguished from these as being plants which regularly grow on other plants, and show more or less special adaptation to the epiphytic habit in the possession of clinging roots, etc. Epiphytic flowering plants are not numerous in temperate regions, their true home is in the damp forests of the tropics

In the tropics, the presence of epiphytes depends chiefly upon the constant dampness of the atmosphere. They are consequently abundant in such a place as Singapore or the south of Ceylon, or again in the Sikkim Himalaya, and very rare or non-existent in the dry plains of India. In tropical America it has been noticed that the epiphytes of the highest tops of the forest trees, *i e.* those which have the greatest development of xerophytic character, appear also as epiphytes upon the drier grassy plains in places where there are trees, this is less marked in India, but a few orchids may be found in such situations. In general, the epiphytic habit seems to be an expression of the struggle for light, and is consequently only necessary in the shady forests As examples of Indian epiphytes may be mentioned numerous Ferns (*Platycerium*, *Polypodium*,

Drymoglossum, and Hymenophyllaceæ), Mosses, Liverworts (especially Jungermanniaceæ), and Lichens (e g. *Usnea barbata*, which forms beautiful grey festoons in the Himalayan forests). Of flowering plants, Orchids and Aroids are among the most important epiphytes.

Climbing plants are characterised by their rapid growth, which enables them quickly to reach the light, and by the feeble development of supporting or strengthening (sclerenchymatous) tissue Although many examples occur in temperate climates, climbing plants are found in the greatest profusion in tropical forests, where, while all four types of climbing are well represented, hook-climbers with sensitive hooks, and root-climbers are specially well shown.

§ 22. **Arctic and Alpine Plants.**—The upper regions of the Himalaya are so lofty that they reach well into the region in which the climate may be regarded as arctic—the chief difference is that the sun, though more powerful, does not shine for so great a part of the day. The flora of both regions is characterised by the small size of the plants, by the dwarfing of shrubs and bushes, and by the relative abundance of mosses and lichens. The stunted growth of the plant is generally supposed to be due to the retarding action of light, exposure to wind, etc Most of the plants also show xerophytic adaptations in the form of crowded, narrow, fleshy or hairy leaves, thick cuticle, etc, for the low temperature retards root-absorption, while the conditions of light, low pressure, and high winds favour increased transpiration. Vegetative reproduction is common, and many of the flowers are either wind- or self-pollinated.

Some of the well-known alpine Himalayan plants are cushion-like species of *Androsace* and *Arenaria*, *Meconopsis*, the Blue Poppy, *Leontopodium alpinum*, the Edelweiss of the Swiss Alps; *Saussurea gossypifera* and *S obvallata*, the latter having a strong smell which is believed to hasten the symptoms of mountain-sickness, species of *Corydalis*, *Potentilla*, *Isopyrum*, and *Primula* The upper limit of tree vegetation is marked by stunted bushes of *Rhododen-*

dron, *Juniperus*, and wild Roses, and by *Betula bhojpatra*, among others.

A marked feature of the alpine flora, or even the floras of the mountain tops when these, as in the Nilgiris, do not reach the truly alpine region, is the presence in them of many **endemic species**, *i.e* species confined to one definite locality, either one mountain or a group of mountains. The explanation of this fact is doubtful; it would appear perhaps most probable that these species were developed each in the place occupied by it, from some common species which ascended the mountains, whether in the ordinary course of migration, or forced upwards by the warmer climate that followed the glacial period, during which many genera of arctic and alpine origin occupied large areas in the plains.

§ 23. **Forest Vegetation.**—In the untouched regions of the tropics, wherever the climate is sufficiently damp, the surface of the ground is covered with lofty forest, whose composition varies much from district to district In the dampest regions, as in the Malay Peninsula or south Ceylon, the forest is very dense, whereas in the dry regions of north India the forest is more what would be termed a park in England, with the trees comparatively widely separated, so that plenty of light gets in between them. In the Himalayas, however, enormous areas are covered with a dense forest consisting principally of Conifers, Oak, and Rhododendron Light is a very important factor in the biology of a forest, and where, as in the damp equatorial regions, the forest is very dense, so that under the trees it is comparatively dark, comes into play in a very marked manner. The typical shape of the trees illustrates this, they have no branches down below, but run up in tall straight boles to the average height of the forest, and branch out at the top.

Climbing plants are very numerous, and grow rapidly up to the light, spreading out at the tops of the trees. Epiphytes similarly abound over the summit level of the forest, and the only plants to be seen in the lower parts are the shade-loving species, which in general belong to two

classes, the smaller trees and shrubs, and the herbaceous plants upon the ground. A good many epiphytic ferns are often to be seen in these lower parts of the forest, but not the more xerophytic epiphytes, which are at the top. Proceeding further north, into the drier parts of the country, the forest becomes less dense, the xerophytic epiphytes disappear from the top and appear, but less commonly, on the lower parts of the trees, and the shade-loving plants gradually disappear altogether, their places being taken by grasses and other ordinary plants of the plains.

Some parts of the North-west Himalayan forest region are interesting in showing a well-marked **altitudinal zonation** of the trees As we ascend from a height of about 3,000 feet we meet successively with different species of Conifers and Oak which characterise more or less well defined altitudinal belts. Another striking feature in the landscape is that the southern slopes of the hills are generally bare of trees, while the northern slopes are forest-clad, the line of demarcation being often very sharp

§ 24. **Field Observations.**—It cannot be too strongly insisted upon, that outdoor observations are absolutely essential in studying the distribution of plants and their adaptations to environment. To study Plant Ecology with success it is necessary to have a good general knowledge of wild flowering-plants, which can only be acquired by collecting and identifying, as far as possible, all the plants met with. At first attention may be confined to the common plants (such as are dealt with in Chapter XIII.). and to those which show well-marked adaptations to their environment, and which occur chiefly in sharply defined "plant associations," *e g.* water-plants, heath-plants, coast-plants

The student cannot do better than begin field observations on some definite and fairly uniform area (*e g* a sea-shore, pond, marsh, river-bank; portion of moorland, meadow, cultivated field or garden with its weeds, forest, wood or plantation with its trees and undergrowth, etc.).

Study this area at all times of the year, identify as many of the plants as possible, and keep a careful record, with sketches, of your observations. The following hints will suggest the main lines on which the inquiry should be conducted; others will occur as your field-work progresses

(1) Physical and climatic features of the area under observation (*e g* chemical and physical nature of the soil; whether retentive and ill drained or porous and well drained, height above sea-level; exposure to, or shelter from, light and wind, etc)

(2) List of the most abundant plants in the area, with notes (and sketches) on the following points in each case — General habit and mode of life (whether annual, perennial, erect, creeping, climbing, xerophytic, aquatic, saprophytic, parasitic, etc), size, form, texture, etc, of leaves; structure of flowers, with special reference to mode of pollination, structure of fruits, with special reference to mode of seed-dispersal, quantity of seed produced, etc

(3) Reasons why certain species are present in the area under consideration and absent from neighbouring areas, and *vice versâ*. To determine these, compare the physical features of the different areas, and try to map out the whole district into regions characterised by definite plant associations, which will, of course, be found to merge into one another at their edges

PART IV.—THE LOWER CRYPTOGAMS.

CHAPTER XX.

LIVERWORTS AND MOSSES.

§ 1. The Group **Bryophyta** or **Muscineæ** is divided into two Classes—the **Hepaticæ** or *Liverworts* and the **Musci** or *Mosses* (see p 5). We shall consider *Marchantia* as a type of the former, *Funaria* as a type of the latter.

A. Marchantia Polymorpha

§ 2. **External Characters and General Life History** (Fig. 273).—The plant, which is found on damp ground, most frequently by the side of ditches, streams, and springs, is a green dorsiventral *dichotomously branching* **thallus** (p. 7), giving off numerous unicellular, hair-like rhizoids from its under (ventral) surface, which also bears violet-coloured flattened scales (*amphigastria*) consisting of a single layer of cells The thallus has a distinct midrib. Special erect **reproductive branches** spring from the upper (dorsal) surface of the thallus. These bear the **sexual organs**, antheridia and archegonia It follows that *the plant is the gametophyte*, and, notwithstanding the difference in the size, the branching, and the position of the sexual organs, is equivalent to, *i e.* homologous with, the prothallus of the Fern. This is an important point which must be carefully borne in mind.

The branches bearing antheridia are called **antheridiophores**; those bearing archegonia, **archegoniophores.**

They are borne on different plants, so that Marchantia is diœcious * Each consists of a stalk bearing a terminal disc or head, **the receptacle.** In both cases the stalk has two furrows which bear rhizoids The *receptacle* of the male shoot is rounded and flattened and has a wavy margin; that of the female is star-shaped, bearing a number of spreading rays resembling the ribs of an umbrella.

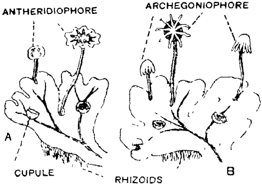


Fig 273 —MARCHANTIA POLYMORPHA
A, Male plant, B, Female

The oospore produced by the fertilisation of the oosphere of the archegonium develops into a structure called the **sporogonium,** which gives rise to **asexual spores.** From the asexual spore a new gametophyte is produced Evidently the sporogonium is the homologue of the **sporophyte** of the higher plants. It consists of a capsule borne on a stalk at the base of which is an absorbing organ called the *foot* It thus shows a rudimentary differentiation into root (foot) and shoot (stalk and capsule), but the shoot is not differentiated into stem and leaves. The sporophyte generation in Liverworts is parasitic on the gametophyte.

The gametophyte reproduces itself *vegetatively* by means

* Many species of Liverwort are monœcious.

of **gemmæ,** multicellular bodies developed in circular cup-shaped organs with membranous margins, called **cupules,** or gemma-cups, formed on the upper surface of the thallus (Fig 273).

§ 3. **The structure of the thallus** is shown in Fig. 274. The great bulk of the thallus is composed of thin-walled parenchyma. The cells towards the lower surface show

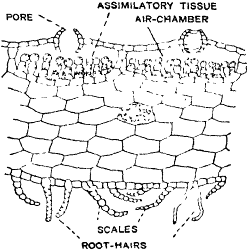


Fig 274.—THALLUS OF MARCHANTIA. (Transverse section)

reticulate markings on their walls. Those nearer the upper surface often contain numerous starch-grains. Here and there single cells with mucilaginous or oily contents occur The upper superficial layer of cells (so-called "epidermis") contains chloroplasts, there is no cuticle Immediately beneath it there are large diamond-shaped **air-cavities** separated from each other by thin cellular partitions which connect the superficial layer with the underlying parenchyma. Short branched rows of small oval cells packed

with chlorophasts grow up **from the floor of each air-cavity**; these form the chief **assimilating tissue** of the plant.

In the middle of the roof of each cavity there is a large **pore** (Figs. 274, 275), bounded by several tiers of cells. Corresponding to the air-spaces the surface of the thallus is marked out into a number of diamond-shaped areas, in the middle of each of which the pore shows as a dot. The pores differ altogether from stomata in their development, although they are analogous organs having the same function. True stomata are not developed on any gametophyte. The absence of vascular tissue should especially be noticed (see p. 20)

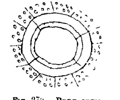


FIG 275.—PORE SEEN FROM ABOVE.

The ventral scales and rhizoids are developed more especially on the midrib. The scales have sometimes been regarded as leaves. The rhizoids in Marchantia are of two kinds —(*a*) long slender hairs, with curious peg-like thickenings developed internally on their walls; (*b*) stouter hairs without thickenings. These rhizoids absorb inorganic solutions in the usual way and fix the plant to the soil.

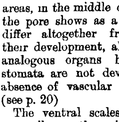


FIG 276.—GEMMA OF MARCHANTIA. (Surface view)

The growth of the thallus is effected by a group of initial cells at each growing-point.

§ 4 **The Gemmæ** (Fig. 276) are flattened isobilateral bodies with a notch on each side. They are developed from single superficial cells of the thallus. Most of the cells contain chloroplasts, but here and there are larger clear cells, which are capable of forming rhizoids. The growing-points are situated in the notches and grow into new thalli.

§ 5 (a). **The Antheridiophore** (Fig 277).—The lower surface of the receptacle of the antheridiophore bears rhizoids and scales like the thallus. The upper surface

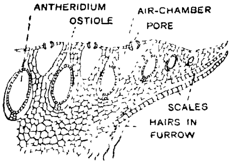


Fig 277.—PART OF ANTHERIDIOPHORE OF MARCHANTIA. (Vertical section of receptacle)

is flat. The tissue of the receptacle is similar to that of the thallus. Air-cavities are present, opening by means of pores on the upper surface. But in addition to these there are large **flask-shaped cavities,** also opening by small apertures called **ostioles** on the upper surface. These cavities are arranged in rows radiating out from the centre, and an **antheridium** is developed on the floor of each. The antheridium (Fig. 278) consists of an oval capsule borne on a short multicellular stalk. The wall of the capsule consists of a single layer of cells containing chloroplasts. Inside there is a mass of **spermatocytes,** each of which gives rise to a bi-ciliate **spermatozoid.**

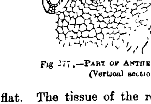


Fig 278 —ANTHERIDIUM OF MARCHANTIA.

In the development of the antheridium a cell grows out from the upper surface of the young receptacle, and is immediately divided

into two. The upper cell forms the capsule; the lower, the stalk. By a series of divisions the wall of the capsule is marked off from a group of central cells from which the spermatocytes are developed The antheridium is gradually enclosed in a flask-shaped cavity owing to the growth of the surrounding tissue. The spermatozoid is developed, as in the Fern, chiefly from the nucleus of the mother-cell, and at first bears a posterior vesicle (see p 354).

§ 5 (*b*) **The Archegoniophore** (Fig 279).—The tissue of the receptacle of the archegoniophore is similar to that of the thallus There are large air-cavities opening by pores on the upper surface, and large mucilage-cells are present The **archegonia** are developed on the under surface of

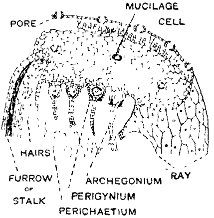


Fig 279 —ARCHEGONIOPHORE OF MARCHANTIA.
(Section between two rays)

the receptacle. They are arranged in radial rows which alternate with the rays of the receptacle The youngest lie nearest to the stalk of the archegoniophore. The margins of the rays grow down and form curtain-like membranes, the **perichætia,** which envelop the archegonia.

The *archegonium* is borne on a short stout stalk and consists of a dilated **venter** and a very long **neck.** The wall of the venter consists of one layer of cells. It

contains the **oosphere** and the **ventral canal-cell.** In the canal of the neck there is a row of **neck-canal-cells.** The neck consists of six longitudinal rows of cells surrounding the canal The terminal cells, called **lid-cells,** are at first united, so that in the young archegonium the apex of the neck is closed. When the archegonium is mature the ventral canal-cell and the row of neck-canal-cells become disorganised, and are converted into mucilage which absorbs water, forces open the lid-cells and oozes out of the neck

The archegonium is developed as a protuberance from a single cell (Fig 280) This grows out and is cut off by a wall. It is then divided transversely into two. The basal cell undergoes a few divisions and forms the stalk The other cell is the mother-cell of the archegonium. It is divided by three longitudinal walls into three *peripheral* cells and one *central* cell. The central cell overtops the peripheral cells, and its apical portion is cut off as the lid-cell, which afterwards by further division forms the lid-cells of the neck The peripheral cells are further divided longitudinally into six, which are called *envelope-cells* The six envelope-cells and the single central cell are then divided transversely into two storeys. The lower storey forms the venter; its envelope-cells further divide to form the wall; its central cell divides into oosphere and ventral canal-cell The upper storey forms the neck; *its* central cell forms by division the row of 8—16 neck-canal-cells.

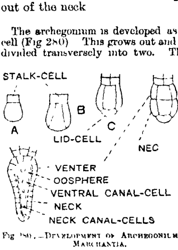


Fig 280.—Development of Archegonium of Marchantia.

§ 6. **Fertilisation and Development of Sporogonium** (Fig 281).—Fertilisation takes place when the plants are wet with rain or dew, and is effected in exactly the same way as in the Fern. The antheridium bursts at the apex, and the spermatozoids are set free. They are attracted to the archegonia by some proteid substance present in the

mucilage which oozes out of the neck. The effects of fertilisation are not confined to the oospore. The whole archegoniophore elongates and becomes very much larger (cf. fruit-formation in Flowering Plants). The venter of the archegonium continues to grow; it is now called the **calyptra**, and forms an investment round the developing **embryo**. A loose cup-shaped structure, the **perigynium**,

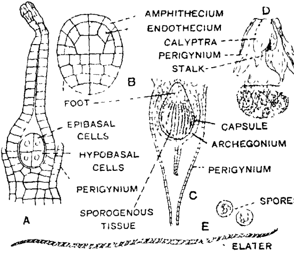


Fig 281 —SEGMENTATION OF OOSPORE AND DEVELOPMENT OF SPOROGONIUM OF MARCHANTIA.

which makes its appearance just before fertilisation (Fig 279) as an outgrowth of the stalk at the base of the archegonium, also grows rapidly and surrounds the calyptra and embryo

The oospore is first divided transversely by a basal wall into an upper or **epibasal** and a lower or **hypobasal cell** (A). Then two other walls, at right angles to each other and to the basal wall, divide the oospore into **octants** (cf. the Fern). The hypobasal octants being further divided give rise to a short bulbous **foot** (B) which absorbs

nourishment from the receptacle (cf Fern), and a short **stalk** which is produced rather late in development by intercalary growth. The epibasal half forms the **capsule** of the sporogonium. By a wall formed parallel to the surface in each epibasal octant a central region, the **endothecium**, is marked off from a peripheral layer, the **amphithecium** (B). The wall of the capsule, consisting of a single layer of cells, is formed from the amphithecium.

The whole of the endothecium constitutes the **archesporium**. Some of the cells produced by the division of the archesporial cells are sterile, they become elongated, spindle-shaped, and spirally thickened. These curiously modified cells are called **elaters** (E), they are hygroscopic, and when the sporogonium opens they aid in scattering the spores. The other cells produced from the archesporium are **spore-mother-cells.** Each gives rise exactly as in the Fern to four **spores.**

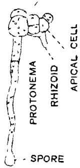


Fig 282 — PROTONEMA OF MARCHANTIA, SHOWING YOUNG THALLUS DEVELOPING FROM GERM-DISC.

Eventually the capsule breaks through the archegonium (calyptra) owing to the elongation of the stalk. It splits longitudinally into a number of divisions or teeth, and the spores are set free (D).

§ 7 **Germination of the Spore** (Fig. 282) —At germination the *exosporium* is ruptured, and the *endosporium* grows out to form a short tube (germ-tube). The further growth of this is at first filamentous, but eventually a small green cellular plate (germ-disc) is produced. The whole structure is called the **protonema.** The young Marchantia plant arises from this *as a lateral outgrowth*. The protonema then dies. It will be noticed that the development of the "plant" is **indirect** or **heteroblastic.** It is preceded by a **pro-embryo,** the protonema.

The life-history of Marchantia is represented graphically in Fig. 283.

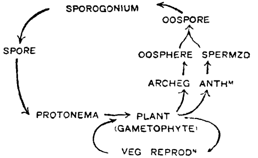


Fig 283 —LIFE HISTORY OF MUSCINEÆ.
In Marchantia the gametophyte is represented by two plants.

B FUNARIA HYGROMETRICA.

§ 8 **External Characters** (Fig 284) —*Funaria* is a common moss which grows in dense tufts or patches on the surface of the ground, often on the tops of walls The plants are small, being scarcely half an inch in height. They are differentiated into stem and leaf (leafy shoot), but there is *no true root*. The dark-coloured base of the shoot gives off numerous slender, brown, *multicellular* **rhizoids,** which pass down into the soil. The leaves are simple and more or less ovate They show a distinct midrib, and have a $\frac{3}{8}$ spiral phyllotaxis. There is comparatively little branching: it is lateral, but not axillary; the branches are given off beneath the leaves.

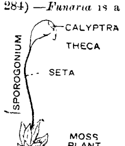


Fig. 284.—FUNARIA WITH SPOROGONIUM

§ 9. **General Life-history.**—The plant, as in the Hepaticæ, is the **gametophyte**, but is much more highly differentiated In the Mosses the gametophyte attains a high degree of development. The **antheridia** and **archegonia** are borne at the apices of the shoots, concealed amongst the leaves of the apical bud (Fig. 286). *Funaria* is monœcious The apical buds containing antheridia can be more or less easily distinguished, as their leaves spread out and form rosette-like structures called **perigonia** or *perichætia*. The central leaves of the rosette are often reddish in colour. The shoots bearing archegonia spring from the bases of the male shoots; their apical buds are not specially distinguished.

It should be carefully noticed that the stem and leaves of the moss are not homologous with, but only analogous to, the stem and leaves of the fern-plant; they belong to different generations

In Mosses, as in Hepaticæ, the sporophyte generation is represented by a **sporogonium** derived from the fertilised ovum. The sporogonium (Fig. 284) is rather more highly differentiated, and consists of a **capsule** or theca, a stalk called the **seta**, and a **foot**.

The asexually produced spore gives rise to a **protonema** (Fig 291), which, however, is a much larger and longer-lived structure than that of Hepaticæ. It is a much-branched filament bearing an external resemblance to a green alga. The cells of most of the branches contain numerous chloroplasts, while others pass down into the soil, and are not to be distinguished from rhizoids. The rhizoids of many mosses may in fact form protonemata The **moss-plant** is developed on the protonema as a lateral bud. The protonema continues to grow for some time, and produces numerous plants Thus, as in Hepaticæ, the development of the gametophyte from the asexual spore is *indirect*

Funaria has great powers of **vegetative reproduction.** Protonemata may be produced from any part—rhizoids, stem, leaf, and even from the sporogonium. In the last case we have an instance of **apospory** (p 359). Some mosses form multicellular *gemmæ*, but this is not the case in *Funaria*.

§ 10 **Structure of the Stem** (Fig 285) —The outermost layer of cells of the stem is marked off as an "*epidermis*" Beneath this is a many-layered **cortical region**, surrounding a **central strand** of elongated thin-walled cells

The cells of the cortex contain chloroplasts, and in the outer region their walls are thickened The central strand



Fig 285 —STEM OF A MOSS
(Transverse section)

is a conducting tissue, and must be considered as representing a rudimentary *vascular cylinder*, *analogous* to the stele of the sporophyte in higher types. In some mosses, such as *Polytrichum*, but not in *Funaria*, the conducting strand shows a central region of thick-walled cells surrounded by a region of thin-walled cells This would be analogous to the differentiation into xylem and phloem.

The growth of the stem in Mosses is effected by a three-sided apical cell like that of the Fern The segments cut off from it divide into inner and outer halves, of which the former give rise to the central conducting tissue Each outer half is divided into upper and lower parts. The upper part protrudes as a two-sided apical cell, and develops into a leaf The lower part forms the cortical tissue of an internode. If branching occurs, the branch is formed from this lower part.

§ 11. **Structure of the Leaf** (Fig 286).—Except at the midrib the leaf consists of a single layer of cells containing chloroplasts This is the **assimilating tissue.** The leaf is thickened at the midrib, which contains a strand of thin-walled conducting cells like those of the stem. In some

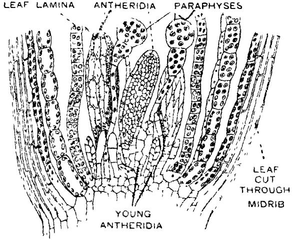


Fig 286.—Apex of Male Shoot of Funaria (Longitudinal section)

mosses these strands join on to the central strand of the stem, but in *Funaria* this is not the case, here there are no leaf-traces.

§ 12 **The Antheridia** (Figs. 286, 287 A) are club-shaped bodies, borne on stout multicellular stalks The wall of each consists of a single layer of cells, within which are numerous **spermatocytes.** On the access of water the antheridium bursts at the apex, and the spermatocytes are liberated Their walls become mucilaginous, and the **spermatozoids** (Fig 287, c) escape. They are biciliate like those of Hepaticæ

The antheridia are developed from single cells at the apex of the shoot, including even the apical cell. The cell grows out, and is divided into two. The lower cell forms the stalk. The upper grows like an apical cell, and gives off two series of segments, which are divided into central cells, from which the spermatocytes are developed, and peripheral cells forming the wall. This mode of apical growth, which is characteristic of Mosses, is unusual

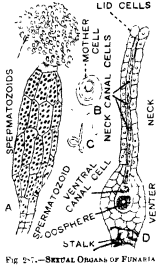


FIG 287.—SEXUAL ORGANS OF FUNARIA A, Antheridium, D, Archegonium

§ 13 **The Archegonium** (Fig. 287, D) is like that of Hepaticæ; but the stalk is more strongly developed The wall of the venter consists of two layers of cells. There is a long twisted neck, consisting of six longitudinal rows of cells, surrounding the central canal.

The archegonium (Fig 288) is developed from a single cell, which may be the apical cell of the shoot. The cell grows out, and the protuberance is divided into two. The *lower cell* forms the stalk. The *upper cell* functions as an apical cell. It shows continued growth, and gives off segments forming, after further division, tiers of cells, each tier consisting of a central cell and surrounding peripheral cells The lowest central cell forms the oosphere and ventral canal-cell; the other central cells form the neck-canal-cells. The peripheral cells form the cells of the neck and venter. Here also the continued apical growth is highly remarkable.

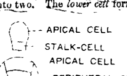


FIG 288.—DEVELOPMENT OF ARCHEGONIUM OF MOSS

The ventral canal-cell and neck-canal-cells are to be regarded as functionless female gametes

§ 14. **Fertilisation** is effected in the usual way. The spermatozoids make their way to the archegonia when the plants are wet with dew or rain. The attracting substance here seems to be cane-sugar. The oospore develops into the sporogonium.

§ 15. **Structure of Sporogonium** (Fig 284) —The sporogonium representing the sporophyte generation is differentiated into root and shoot, but not into stem and leaves. It consists of foot, seta, and capsule. The **foot** (Fig 290, E) is a small conical structure which buries itself in the apex of the female shoot, and serves for the absorption of nutriment It is invested by a membranous sheath, the **vaginula,** representing the lower half of the archegonium, which is ruptured during the development of the sporogonium The **seta** is a long slender structure of a reddish colour. It has an "epidermis," a thick-walled cortex, and a conducting strand like that of the moss-plant

The **capsule** (Fig. 289) is a pear-shaped structure. Its solid basal region is called the **apophysis.** The epidermis of the apophysis has *true stomata* At each end of the pore the wall between the two guard-cells breaks down, so that the pore seems to be surrounded by a single ring-shaped cell The parenchymatous cells beneath the epidermis contain chloroplasts The conducting strand of the seta is continued into the apophysis It has been proved that the sporogonium can assimilate all the carbon that it requires, so that only inorganic solutions are absorbed by the foot. It may be regarded as only semi-parasitic

The **wall** of the capsule consists of several layers of cells, the inner layers contain chloroplasts. Internal to this is a large **air-space** traversed by delicate strands of cells. Next comes the **spore-sac,** surrounding a sterile central column, the **columella.** The outer wall of the spore-sac consists of two or three layers of cells. The inner wall lies next the columella

At the apex of the capsule is a sort of lid, the **operculum,** which separates off when the capsule dehisces The dehiscence is effected by the rupture of a ring of

cuticularised epidermal cells, the **annulus**, round the base of the operculum, immediately above the upper end of the spore-sac. When the operculum comes away a number of yellow, thickened, tooth-like structures, constituting the

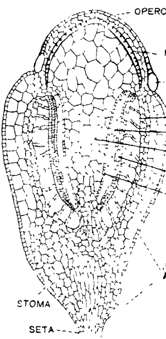


Fig 258.—CAPSULE OF FUNARIA.
(Longitudinal section)

peristome, project. These are hygroscopic, and allow the spores to escape only when the air is dry. In *Funaria* there are two rows of peristome teeth (outer and inner). They represent the outer and inner thickened and cuticularised regions of the walls of a plate of cells which have otherwise broken down The sixteen outer teeth of the

peristome are joined at their tips by a small disc of tissue. The apex of the capsule is covered by a membranous cap, the **calyptra** (Fig. 290, E), representing the upper half of the ruptured archegonium

§ 16. **Development of Sporogonium** (Fig 290).—The oospore is first divided by a **basal wall** into **hypo- and epi-basal cells.** By further division a two-sided apical cell is formed at each end The two rows of segments cut

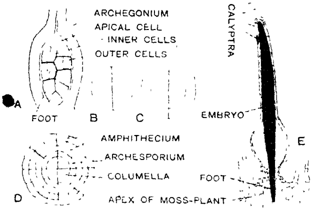


Fig 290 – DEVELOPMENT OF SPOROGONIUM OF FUNARIA
B, C, D, transverse sections, D, in region of Capsule

off from the apical cell at the hypobasal end form the foot (A) The epibasal half also forms two rows of segments (A, B). The segments are divided into outer and inner halves (A, C). In the region of the seta the inner halves form the central conducting tissue, the outer halves the cortical tissue In the region of the capsule, which is not distinctly marked off from the seta till the embryo has elongated considerably, the outer halves constitute the **amphithecium**; the inner halves the **endothecium** (D).

The **archesporium** is the *outermost layer* of the endothecium, the rest of the endothecium forming the columella.

Everything outside the sporogenous tissue, including the outer wall of the spore-sac, is derived from the amphithecium. The operculum slowly differentiates, and the innermost layer of the amphithecium over the region covered by the operculum gives rise to the peristome. The archegonium is ruptured during the elongation of the sporogonium The **spores are developed from the mother-cells** in the usual way. There are no elaters

§ 17. **Germination of the Spore** (Fig 291) —When the spore germinates, the exosporium is ruptured and the endosporium grows out at each end into a germ-tube At one end the germ-tube forms a **rhizoid.** The other develops into the **protonema.** The growth of each branch of the protonema is effected by means of its apical cell.

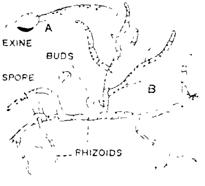


Fig 291 —A, GERMINATING SPORE. B, PROTONEMA OF FUNARIA.

§ 18 **The Young Moss-plant** (Fig 291) arises as a little bud from a cell of the protonema close to a septum. In this protuberance oblique divisions appear, and these separate the apical cell of the young plant from those which give rise to the first leaf and the first rhizoid

The life-history is represented graphically in Fig 283

§ 19. **Summary and Conclusions.**—Thus, in the Bryophyta, there is a distinct alternation of generations The gametophyte is *the plant*; the sporophyte generation is represented by a sporogonium parasitic or semi-parasitic on the gametophyte. The relative importance of the two

generations has been reversed as compared with what we find in Vascular Cryptogams and Flowering Plants. The sporophyte is practically only a sporogenous capsule; there are no distinct sporangia. A seta is developed simply to elevate the capsule, and a foot to absorb nourishment.

It is only in some Liverworts that the plant-body is a thallus; in the great majority it is differentiated into stem and leaves. In Liverworts the protonema, if developed at all, is small and short-lived, elaters are usually present, and, except in a few cases, there is no columella. In Mosses the protonema is well developed; there is a columella, but no elaters.

Antheridia and archegonia are the characteristic sexual organs of the Bryophyta and Pteridophyta. For this reason the two groups are together spoken of as the *Archegoniatæ*.

§ 20. **Relationship of Bryophyta to Pteridophyta.**—There is a very wide gap between the Bryophyta and the Pteridophyta—wider even than that between the Pteridophyta and Phanerogams. Nevertheless, the homologies discernible between the two groups—*e.g.* the alternation of generations, the similarity in the *general* course of the life-history, the development of the spores, etc.—leave no doubt that they are genetically connected, in other words, that the two groups are descended from common ancestors. There is reason to believe that the thalloid Hepaticæ are the living forms which most nearly approach the primitive ancestral forms. While the Pteridophyta would represent the main line of evolution along which the sporophyte became more highly differentiated, the Liverworts and Mosses would represent divergent lines along which the gametophyte attained a comparatively high development.

§ 21. **Origin and Evolution of the Sporophyte.**—A consideration of the simple organisation of the sporogonium of Bryophyta naturally suggests questions as to the origin of the sporophyte generation, and to the stages through which it passed in the course of its evolution till it became the conspicuous generation (the plant) in the higher groups.

It is now held by many that the sporophyte is a stage in the life-history intercalated in the course of evolution between two successive gametophytes, and that its origin and development are associated with the adaptation to aerial conditions which ensued when the primitive aquatic plants began to encroach on the land. We may assume that in these primitive plants, as in many Algæ at the present day, there was no sporophyte, and that the oospore

developed immediately into a new gametophyte. In this case the reduction in the number of chromosomes (reducing division, p 44) would take place at the first division of the oospore. The first step in the development of a sporophyte, initiated probably by the reducing division being delayed, consisted, it is believed, in the oospore breaking up into a number of small spores each capable of giving rise to a gametophyte. Examples of such subdivision are found in many Algæ, and its advantage to plants beginning to encroach on conditions which endangered the fertilisation process is obvious.

As adaptation to land conditions proceeded there would doubtless be an increase in the number of spores, as an increased output would be an advantage in the struggle for existence. This increase, however, could not go on indefinitely unless suitable provision were made for the nourishment, protection, and scattering of the spores. The further progress of the sporophyte cannot be traced with any certainty, but a study of the sporogonium in Bryophyta suggests what are believed on various grounds to be the more important factors in the process.

In *Riccia*, one of the simplest Liverworts, the sporogonium is simply a spherical capsule containing spores. In most of the Bryophyta, however, there is a distinction of base and apex and a foot is developed. In the Liverworts the function of the elaters is partly to nourish the spores, and partly to help in their dispersal. The central columella of Mosses serves as a tissue conducting nourishment, and, owing to its development, the spores are produced from the more external tissues, with the result that their dispersal is facilitated. These parts, foot, elaters, columella, have evidently been derived from tissue originally sporogenous. Here we trace the beginnings of the vegetative system in the sporophyte; owing to its development the formation of spores is postponed, their immediate formation being no longer an urgent necessity. In most Liverworts nourishment is supplied chiefly by the gametophyte, but in *Anthoceros* and in Mosses the capsule contains chlorophyll and bears stomata, so that the sporophyte largely helps in providing nourishment.

So far we have recognised what are regarded as three important factors in the evolution of the sporophyte.—(*a*) sterilisation of tissue originally sporogenous, leading to the development of a vegetative system; (*b*) the consequent postponement of spore-production; (*c*) the superficial development of spores owing to sterilisation of central tissue.

Along the Pteridophyte line, however, the operation of these factors was supplemented by that of others, which have been indicated by various converging lines of evidence —

(1) Provision was made for more extensive formation of vegetative tissue, and further postponement of spore-formation by the development of an apical growing point. In this connection the growth of the sporogonium of Mosses by means of an apical cell should be noticed.

(2) The nutrition of the spores was undertaken more and more completely by the sporophyte. The development of leaves and roots would be correlated with this. The root was undoubtedly a secondary formation evolved in response more especially to the necessity for securing an adequate supply of water. We can readily conceive the primitive sporophyte borne on a thalloid gametophyte sending down absorbing organs into the soil. During the early imperfect stages of evolution the foot would continue to carry on its absorbing functions, but gradually its period of functional activity would be restricted to embryonic stages. The leaves no doubt originated as small, lateral outgrowths of sterile tissue providing for increased assimilation.

(3) It is probable that the actual sporogenous tissue was now, owing to further sterilisation, segregated in small masses or pockets, which, for reasons already given, would be developed from the superficial tissues, and, for protection, would naturally be associated with the leaves. Here we have the origin of sporangia.

We may now conceive of the shoot of the primitive sporophyte as a radial axis with an apical growing point, and bearing numerous small leaves with which the sporangia were associated. The leaves therefore were sporophylls. As the vegetative system became more extensive it is probable that in the lower part the sporangia disappeared, and the leaves in that region came to have purely vegetative functions. A condition not much more advanced is found in some primitive existing species of Clubmoss (*Lycopodium*, e.g. *L. Selago*). The indefinite extension of the vegetative system, with consequent postponement of spore formation, being provided for by continued apical growth, and later by branching of the axis, it is probable that the sporophylls came to be more and more restricted to the upper parts of the plant.

While this was the probable course of development along one line of evolution, there were no doubt variations along other lines. In the Ferns, for example, we have a group in which the leaves apparently underwent a great development, and continued, to a large extent, to function as sporophylls (with numerous sporangia). In this connection it should be noticed that, if the Angiosperms are really descended from fern-like ancestors (p. 410), their sporophylls must not only have undergone specialisation, but also extensive reduction in size and complexity.

§ 22. **Sporophylls and Foliage Leaves.**—Till recently it was generally believed that sporophylls were derived from foliage leaves, which in the course of evolution began to develop sporangia, and, being thus set apart, as it were, for reproductive purposes, underwent extensive modification. This view can no longer be regarded as tenable if the course of evolution has been on the lines described above. Indeed, the opposite view would be nearer the mark, for it would seem that the first leaves were sporophylls, and that the foliage leaves were derived from them by suppression of their sporangia.

We may suppose, however, that the primitive leaves combined vegetative and reproductive functions Later these functions were differentiated and the specialisation of foliage leaves and sporophylls proceeded along separate lines The infinite variety of form and organisation exhibited by the foliage leaves of flowering plants must be ascribed to the fact that being purely vegetative organs they are more subject to the modifying influence of external conditions than sporophylls and have therefore undergone more extensive adaptive modification.

CHAPTLR XXI

THE ALGÆ

§ 1 **General Characters** —The Al͏gæ constitute one of the two important Classes into which the Thallophyta are subdivided They are adapted to aquatic or moist conditions Many are fresh water forms, but the great majority live in the sea, and constitute the assemblage of organisms called the marine Algæ or *seaweeds* Many of the lower forms are unicellular In the higher forms the vegetative body is usually a **thallus** but many show a more or less well marked differentiation into root and shoot and some also into stem and leaf Structurally, the thallus consists entirely of living cells, although in some of the larger forms distinct conducting and assimilating tissues are developed.

In essential points the processes of nutrition resemble those of the ordinary green plant while differing widely in detail (see p 15) All the Algæ contain chlorophyll but in many the green colour of the plastids is masked by the presence of other colouring matters These are chiefly a brown colouring matter (phycophæin) * a red colouring matter (phycoerythrin) and a blue colouring matter (phycocyanin) The differences in colour are correlated with important differences in development and life history —hence the convenient division of the Algæ into Green (Chlorophyceæ) Brown (Phæophyceæ) Red (Rhodophyceæ) and Blue green (Cyanophyceæ or Myxophyceæ) The Brown and Red Algæ are mostly marine

§ 2 **Reproduction** —While many of the lower Algæ have only a vegetative method of reproduction by cell division in the higher Algæ sexual reproduction and asexual reproduction by means of spores are both of general occurrence

* According to recent research however the Brown Algæ do not possess a special brown pigment and the so called phycophæin in a watery extract of these Algæ is the result of *post mortem* oxidation changes in an originally colourless substance

It has been found that the production of sexual organs and of spores is largely determined by external conditions. Some conditions favour sexual reproduction, others asexual. Thus, while spores and sexual organs may be produced on the same plant, they are usually found at different times In many cases it can be recognised that sexual reproduction takes place when the conditions for growth are becoming unfavourable, and that the sexually produced spore is of the nature of a resting spore Frequently also it is found that one or more generations of asexual plants may occur before the appearance of a generation which bears sexual organs *

In all cases where sexual reproduction occurs at all, the plant may be regarded as the gametophyte, actual or potential

§ 3 **Asexual Reproduction.**—The spores may be special non-motile cells But frequently, in adaptation to aquatic conditions, they are naked protoplasmic bodies (protoplasts) which move by means of cilia, and are called **zoospores;** in this case they are formed, one or more, by rejuvenescence of the contents of a mother-cell (p 45)

These spores which are produced *on the gametophyte*, or what is regarded as representing the gametophyte, and which directly *reproduce the gametophyte*, are by many botanists called **gonidia,** or, if motile, **zoogonidia,** in order to distinguish them from the spores of the higher plants which are produced on the sporophyte and give rise to the gametophyte Similarly the organ in which they are produced is not called a sporangium, but a **gonidangium.**

* This is quite a different kind of alternation from that found in higher plants The two plants, sexual and asexual, are similar or "homologous," and the asexual plants may be produced for several generations by means of asexual spores. Some Botanists, however, believe that alternation in the higher plants was evolved by the gradual differentiation of two such "homologous" plants, and the modification of the asexual plant in adaptation to aerial conditions This is the **homologous theory of alternation** as distinguished from the **antithetic theory** described on pp 507-510. To some it seems probable that the antithetic theory explains the origin of the Bryophyte sporogonium, and the homologous theory that of the sporophyte of Pteridophyta.

§ 4 **Sexual Reproduction.**—The **gametes** and the **gametangia**, *i e* the organs producing the gametes, may or may not be differentiated into male and female. If the sexual process consists in the conjugation of similar gametes (p 45) it is said to be **isogamous**, and the **zygote** formed is termed a **zygospore**. If it consists in the fertilisation of an oosphere by a male element it is **heterogamous** (as in higher types) and the zygote is an **oospore**. This applies to the Green and Brown Algæ, in the Red Algæ the sexual processes are very peculiar and highly specialised

The zygospore or oospore may develop directly into a new plant (gametophyte); but frequently it either forms a number of spores or zoospores by division or gives rise to a small body in which they are formed This has been regarded as a rudimentary development of a **sporophyte generation,** and the **spores** or **zoospores** so formed are not called gonidia or zoogonidia, although in appearance they are exactly like them.

§ 5 **Alternation of Generations.**—In the Algæ, as in Thallophytes generally, there is no regular fixed alternation of generations The sporophyte is either unrepresented or represented only in a rudimentary form Moreover, it is extremely doubtful if what have been taken to represent gametophyte and sporophyte in the Thallophytes really correspond phylogenetically to the two generations of higher plants.

Remembering the aquatic adaptation of Algæ we may take it that in them a sporophyte, adapted to aerial conditions, has not yet appeared, and that the plant contains within itself the potentialities of both generations We need not wonder therefore that the Algæ can reproduce themselves both sexually and by means of asexual spores. In this connection we may recall the fact that in certain cases fern-prothalli have been found to produce sporangia and spores (p. 359) For these reasons many botanists make no distinction between zoospores and zoogonidia

We have seen that in the higher plants the number of chromosomes in the cells of the sporophyte is double the number in the

cells of the gametophyte. The reduction of the chromosome number is effected at the division of the spore mother-cells.

Recently attempts have been made to discover if anything similar occurs amongst the Thallophytes. A reducing division has now in a good many cases been demonstrated, but it has been found that it does not occur always at the same point in the life-history. Occasionally it takes place at the first division of the oospore; in this case the plant has the reduced number of chromosomes. In other cases it does not take place until the divisions which lead to the formation of the sexual organs, and the sexual plant therefore has the double number of chromosomes (e.g. *Fucus*).

It is, however, an interesting fact that one or two types of Algæ are now known in which a sexual plant with reduced number of chromosomes regularly alternates with an asexual plant having the double number, reduction of chromosomes taking place at the division of the spore mother-cells. This corresponds exactly with what is found in the higher plants except that the two generations resemble each other in appearance and adaptation.

CHLAMYDOMONAS

§ 6 *Chlamydomonas* is one of the unicellular Green Algæ. The genus includes about 30 species, found chiefly in ponds and ditches. There are two phases or stages in the life-history—the motile or normal vegetative stage, and the resting or *palmella*-stage, which is followed by reproduction. The structure of the cell is very constant throughout the genus, but the different species present considerable differences in appearance and mode of life.

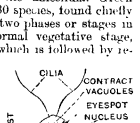


Fig 292 —*Chlamydomonas*
A, Motile Cell, B, Conjugating gametes

§ 7 **Structure of the Cell** (Fig 292, A) —The motile cell is usually more or less spherical or ovoid in shape. It has a cellulose wall which is in close contact with the protoplasmic contents. The protoplasm at the anterior region is clear and hyaline in appearance, and gives off two **cilia** or flagella, which pass through the cell-wall. The protoplasm in this region also has two **contractile vacuoles** (*i.e.* spaces, filled with sap, which

show alternate expansion and collapse), situated at the base of the cilia, and an orange-coloured **pigment-spot** placed laterally. Posteriorly the protoplasm contains a single, large, more or less cup-shaped **chloroplast**, in which is embedded a rounded body known as the **pyrenoid.** A single **nucleus** is present in the central region of the protoplasm inclosed within the cavity of the chloroplast.

The cells move through the water by means of their cilia. The movement is automatic, but it is modified by the action of light and other stimuli. The cells move towards bright diffuse light, away from light of too great intensity. This sensitiveness to light is specially associated with the pigment-spot.

The pyrenoid consists of proteid substances. Its function is not known with certainty. It has been compared with the proteid crystalloids of higher plants and may represent a store of food-material. From the fact that it is frequently surrounded by a layer of starch it has been supposed also that it may play a part in the process of carbon-assimilation. Pyrenoids are frequently found in the cells of Algæ.

The function of the contractile vacuoles is not understood. They may be respiratory organs, or perhaps excretory organs.

§ 8. **Asexual Reproduction.**—Under unfavourable conditions the cells withdraw their cilia, and pass into a resting state in which they may continue for some time. Sooner or later, however, the contents of the cells by repeated division give rise to 4 or 8 protoplasts, which are set free, as **zoogonidia,** by the rupture of the wall of the mother-cell. These, by the secretion of a cell-wall, give rise to the motile vegetative stage again.

§ 9. **Sexual Reproduction** (Fig. 292, B).—The contents of many of the resting cells divide into a greater number of parts—16, 32, or even 64. The resulting motile protoplasts, in form and structure, resemble the zoogonidia, except that they are smaller. They conjugate in pairs, and are therefore of the nature of gametes

(**planogametes,** *i.e* motile or wandering gametes). The gametes are more or less pear-shaped and have two cilia They unite by their pointed ends, and fusion of their protoplasm and nuclei then takes place The cilia are withdrawn and a cell-wall is formed After a period of rest the resulting **zygospore** gives rise to 2 or 4 **zoospores** by division of its contents The zoospores produce the motile vegetative stage again

In one species of *Chlamydomonas* the gametes are differentiated into male and female, the female larger and the male smaller

§ 10 *Chlamydomonas* is interesting because it is believed to be, in many respects, a primitive type It shows affinities to the Flagellatæ, a group of organisms, destitute of a cell-wall, which exhibit both plant and animal characteristics Some of them are holophytic, *i e* they possess chlorophyll and are able to elaborate their food-material from simple inorganic compounds Others feed on organic compounds Both animal and vegetable kingdoms are believed to have taken their origin from types resembling the Flagellatæ, and *Chlamydomonas* is supposed to approximate closely to the ancestral organisms from which the whole of the vegetable kingdom has been derived The resting stage of *Chlamydomonas*, accompanied by cell-division, may be regarded as the starting point of the vegetative stage of higher types, the motile vegetative stage of *Chlamydomonas*, in higher types, has persisted only in the reproductive processes.

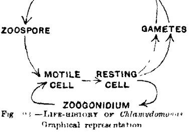


Fig 293 —LIFE-HISTORY OF *Chlamydomonas* Graphical representation

The life-history of *Chlamydomonas* is represented graphically in Fig 293.

HÆMATOCOCCUS (SPHÆRELLA) PLUVIALIS

§ 11 In structure, life-history, and mode of life *Sphærella* closely resembles *Chlamydomonas* (Fig 294). The two genera belong to the same family of Algæ The following are the more important differences —In *Sphærella* the cell-wall is separated from the protoplasmic contents by a space which is traversed by protoplasmic filaments (Fig 294, A), contractile vacuoles are wanting; the cells, more especially the resting cells, frequently contain a red colouring matter, *hæmatochrome*, which gives them a blood-red appearance The resting cells are frequently found in rain-water which has collected in the hollows of rocks, in gutters, or in water-butts

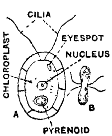


Fig 294 —*Sphaerella* A, Motile cell, B, Conjugating gametes

In *Sphærella* it has been observed that *if the gametes fail to conjugate they may behave like zoogonidia and give rise to motile vegetative cells*

Before the life-history of *Sphærella* was completely known the motile cells were known as *Protococcus pluvialis*

§ 12 *Hæmatococcus* (*Sphærella*) *nivalis*, the Red Snow Plant, is another species closely resembling *H. pluvialis* in structure and mode of life Its resting cells, which contain abundant red pigment, form blood-red patches on the snow in Greenland and in the Alps A red snow alga has also been discovered in the North-west Himalaya (Kashmir)

§ 13 **Origin of Sexuality** —From a careful consideration of the fact, observed in various Algæ, that the gametes resemble the zoogonidia and may behave like them, the conclusion has been reached that gametes have been derived from zoogonidia—that they, in fact, *are* zoogonidia in which the tendency to, and capacity for, conjugation has been evolved On the view that conjugation means increased vigour and vitality, we can understand how this tendency would be evolved In *Sphærella* (and certain other Algæ) it is scarcely a fixed hereditary character, and the gametes may still develop without conjugation *Parthenogenesis* probably represents a trace of this in higher types

Pleurococcus vulgaris

§ 14 This is one of the commonest unicellular Green Algæ, forming the green covering so frequently seen on tree-trunks, palings, etc, after wet weather, more especially on the side most exposed to the wind The Alga was formerly known as *Protococcus viridis*

§ 15 **Structure of the Cell** (Fig 295) —If a little of the green substance be examined in water under the microscope it is found to consist of small green cells, sometimes single, sometimes aggregated into groups or colonies of two, four, or more, owing to the fact that after division the daughter cells do not separate from each other. The individual cells are almost spherical if isolated, but in the cell-groups they are slightly flattened on the sides in contact with the other cells.

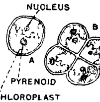


Fig 295 —*Pleurococcus* A, Single cell, B, Group of cells

Each cell has a firm cellulose wall Embedded in the protoplasm on one side is a single, large, lobed **chloroplast** with a well-marked **pyrenoid.** A **nucleus** is present in the centre of the cell

§ 16 **Reproduction.**—The usual method of multiplication is a vegetative one by cell-division and separation of the daughter cells from each other In very moist conditions the cells may not separate, and in this way short filaments of cells may be formed

Asexual reproduction by means of biciliate zoogonidia occasionally takes place, as also does sexual reproduction by the conjugation of similar gametes. The zoogonidia and gametes are formed by rejuvenescence of the contents of the vegetative cells, which then function as gonidangia or gametangia.

§ 17. We have seen that in *Chlamydomonas* and *Sphærella* the motile stage is the ordinary vegetative condition of the Alga—the non-motile stage being a resting condition. It would seem, however, that in the evolution of plants the non-motile condition attained greater importance. It has become the normal vegetative condition in *Pleurococcus*, whose life-history also gives an indication as to how the multicellular structure of higher plants has arisen.

Spirogyra

§ 18 **General Characters.**—*Spirogyra* is one of the green fresh-water Algæ. It grows in bright-green slimy masses in ponds, springs, or slow-running streams. Each *Spirogyra* plant has an extremely simple structure. Its vegetative body is an *unbranched* filamentous **thallus** (Fig. 296), consisting of short cylindrical cells placed end on end and showing no distinction of base and apex. The filament increases in length by ordinary cell-division and growth of the cells. All the cells have the same structure and all are capable of division.

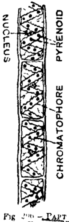


Fig. 296.—Part of a Filament of Spirogyra.

Here we have an example of a multicellular plant which shows little or no division of labour. Indeed, we might, physiologically, regard each cell as an individual plant, and the whole filament as a colony of such individuals, for each cell carries on exactly the same vital functions as are necessary for the maintenance of the whole

The filament is, in most species, invested by a delicate mucilaginous sheath formed from the pectic compounds of the cell-walls It is this which makes a mass of *Spirogyra* filaments feel slimy to the touch

§ 19. **Structure of the Cell** (Fig 296) —Each cell is cylindrical in form with transverse end-walls, and has the structure characteristic of typical parenchymatous cells.

The wall consists of cellulose and pectic compounds Inside the cell there is a "**primordial utricle,**" from which delicate **protoplasmic strands** run across a central **vacuole** to the centre of the cell The **nucleus,** containing a distinct nucleolus, is usually embedded in the small central mass of protoplasm The most conspicuous structures in the cell are the green spirally coiled *chlorophyll bands* or **chromatophores** (chloroplasts). There may be from one to eight of them in a cell, the number varying slightly even in the same species. They lie in the primordial utricle, coiled as it were round the central vacuole Each contains a number of well-marked **pyrenoids.**

Numerous species of *Spirogyra* are distinguished according to the size and form of the cells, the character of the chromatophores, etc

§ 20 **Reproduction.**—There is no special method of asexual reproduction; but if a filament happens to be broken into a number of pieces, consisting of one or several cells, these by ordinary cell-division may form new filaments

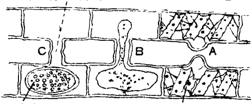


FIG 297.—SPIROGYRA IN CONJUGATION

(vegetative reproduction). Fragmentation of this kind may occur naturally under abnormal nutritive conditions

Sexual reproduction (Fig 297) seems to occur whenever the vigour of the filaments becomes impaired by age, by prolonged division, or by unfavourable external conditions. It is generally **isogamous.** In this process two filaments, lying side by side, send out little outgrowths from corresponding cells. These increase in size, meet, and finally

fuse between the two filaments, so that the corresponding cells are joined by short **conjugation-tubes.** In the meanwhile the contents of each cell have contracted, losing water and forming a **gamete**, in which the characteristic form and appearance of the chromatophores can no longer be distinguished. Then the gametes of one filament pass over, by means of the conjugation tubes, into the cells of the other filament, and fuse with the gametes in these cells.

It should be specially noticed that the gametes bear no cilia (**aplanogametes**), and that any cell of a filament may function as a **gametangium**; also that **conjugation** is effected by means of conjugation-tubes. The more active gametes, which may be regarded as being male, are formed earlier than the more passive ones, which may be considered as female. Generally all the gametes of one filament pass over into the other filament, so that the filaments are unisexual. In *S. inflata* female filaments are distinguished from the male by their much larger cells, so that here we have a further step towards the differentiation of sex. There are, however, exceptions to this, and occasionally, also, conjugation tubes are formed between cells of the same filament. In a family closely allied to *Spirogyra* conjugation is effected in the middle of the tube, and the gametes are in all respects alike.

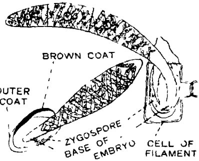


FIG. 298.—SPIROGYRA. GERMINATION OF ZYGOSPORE.

§ 21. **The Zygospore.**—The result of conjugation is in each case the formation of a zygospore (Fig. 297). This is a large oval body, at first green, but later becoming dark brown. After a more or less lengthy period of rest, the zygospores germinate. Each contains food-material

in the form of oil and other substances. In germination the two outer coats of the spore (Fig. 298) are ruptured, and the contents enclosed in the innermost coat grow out into a tube which is divided into two cells by a transverse septum. The cell which protrudes from the spore is green, and grows out to form the filament The other cell is colourless Thus, at first, there is a distinction of base and apex, but this is soon lost.

Sometimes, when conjugation does not take place, a gamete may develop directly into a spore called an azygospore. This may be compared with parthenogenesis (p. 271)

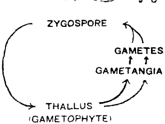


Fig 299 —Graphical Life-history of Spirogyra

§ 22 *Spirogyra* belongs to a group of the Chlorophyceæ known as the Conjugatæ. The plant represents the gametophyte. The sporophytic generation is confined to the zygospore Reduction of chromosomes occurs during the germination of the zygospore, so that the new plant is again gametophytic.

Vaucheria

§ 23 **Structure.**—Most of the species of this green Alga grow in fresh water, or on the damp surface of the soil A few species are marine. *V sessilis* and *V. terrestris* are commonly found, mixed with other Algæ and the protonemata of mosses, in the form of a green tangled felt on the damp soil of neglected flower-pots

The thallus (Fig 300, c) consists of long, rather coarse, tubular threads, branched at considerable intervals, and fixed by means of a branched colourless **root-process.** The tubes are **non-septate,** *i e* they are not divided by cell-walls into distinct cells Septa, however, are formed when the thallus is injured and in connection with the development of reproductive organs. The cellulose wall of each tube has a continuous **protoplasmic lining.** A

vacuole filled with cell-sap runs up the middle of the tube. In the outer region of the protoplasm there are numerous oval **chloroplasts**, and large numbers of small **nuclei** are found in the layer internal to this. There are

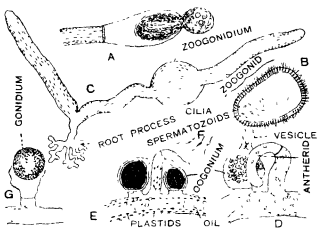


Fig. 300.—VAUCHERIA.
A, B, The zoogonidium; C, Young plant formed from zoogonidium; D, E, F, Sexual organs.

no pyrenoids. Small refractive **oil-globules** are associated with the plastids. It is interesting to notice that usually no starch is present; here the storage product of metabolism is oil.

Vaucheria was formerly described as a *unicellular* Alga. The branched tubes, however, are not cells, but **cœnocytes**; here we have a good example of cœnocytic structure (p. 44). The branches of the cœnocyte exhibit apical growth.

§ 24. **Asexual reproduction** is commonly effected by means of zoogonidia. In the formation of a zoogonidium the apex of a branch swells up and becomes club-shaped (Fig. 300, A), owing to the aggregation of protoplasmic substance in it. This club-shaped body, which is the

gonidangium, is separated from the rest of the tube by a distinct septum. It ruptures at the apex, and the protoplasmic contents escape as a zoogonidium. The opening is very narrow, and, as the protoplasmic body makes its way out, it is frequently constricted and divided into two zoogonidia

The **zoogonidium** (Fig 300, B) is a large oval body which can be seen by the naked eye It shows a central region, containing numerous chloroplasts, and a clear outer region, *the ectoplasm*, with numerous small nuclei. Evidently it also is cœnocytic and might be called a *zoocœnocyte* It is covered with **cilia,** a pair being developed opposite to each nucleus. The zoogonidium, after moving about for a short time, develops a cellulose wall and comes to rest The cilia are withdrawn, and germination takes place Two tubes grow out One branches and produces the colourless root-process, the other develops into the green tubular thread (Fig 300, C).

Some species of *Vaucheria* (not *V sessilis*) produce **gonidia** or non-motile spores. The apex of a tube or short lateral branch swells up and becomes more or less globular This body, the gonidium, is cut off by a septum, and germinates after a longer or shorter period of rest without producing a zoogonidium. Sometimes the gonidium is formed in this outgrowth by rejuvenescence and the formation of a new cell-wall (Fig 300, G).

In unfavourable conditions, such as conditions of drought, the tubes may become septate They are divided up into short segments which develop thick walls It is a resting, protective condition, and has been called the *Gongrosira-condition* On the return of favourable conditions the segments germinate and produce new plants This may be considered as a purely vegetative method of reproduction

§ 25 **Sexual reproduction** is heterogamous (Fig. 300, D–F) The male organ is an **antheridium;** the female organ is called the **oogonium.** They arise as outgrowths, either of the tube itself (*V sessilis*) or of a special short branch, and are usually borne on the same plant The number of oogonia and antheridia associated together varies in the different species In *V sessilis* there is frequently one antheridium between two oogonia (E) A few species are diœcious

The outgrowth which becomes the antheridium contains numerous chloroplasts and small nuclei. As development proceeds the nuclei aggregate in the central region of the protoplasm and give rise to a large number of very minute biciliate spermatozoids The chloroplasts pass to the base of the outgrowth, and are cut off by a septum from the portion containing the spermatozoids, which is the antheridium proper. When fully formed the antheridium is a colourless tubular structure curved like a horn (D). It ruptures at the apex, and the spermatozoids are set free (E, F).

The outgrowth which forms the oogonium at first contains numerous nuclei in addition to chloroplasts One nucleus passes to the centre of the protoplasmic mass, and becomes the nucleus of the **oosphere**; the others pass back into the tube The oogonium is then separated off by a septum A little protuberance or beak appears near the apex It bursts open and a small portion of the protoplasmic contents is given off (D) The rest of the contents form the oosphere, which contains numerous chloroplasts It shows a clear spot—the **receptive spot**—near the beak where the protoplasmic vesicle was given off. The fully formed oogonium is sessile, and more or less ovate in form It has a simple cellulose wall and contains one oosphere It is a much less complex female organ than the archegonium

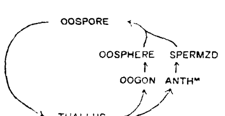


FIG. 301 – GRAPHICAL LIFE-HISTORY OF VAUCHERIA

Fertilisation is effected by a spermatozoid entering the ovum at the receptive spot, and fusing with it. The **oospore** develops a thick wall and enters on a period of rest. When it germinates it produces a new plant directly.

§ 26 *Vaucheria* belongs to a group of Chlorophyceæ known as the Siphoneæ The plant is the gametophyte There is no alternation of generations. Perhaps the most striking feature about *Vaucheria* is the association of highly differentiated sexual organs with a very simple vegetative body. The life-history is graphically represented in Fig 301.

Œdogonium

§ 27 **General Characters.**—*Œdogonium* is a very common green Alga including numerous species, all living in fresh water. Each plant (Fig 302, A) has an *unbranched*, filamentous **thallus**, consisting of elongated cells In young stages (B, C) the plants are attached to stones or other plants by means of a basal fixing organ, but in many species the adult plants are free The apex of the filament may be rounded, or, in a few species, may end in an elongated hair-like process The growth of the filament is effected by division of any of the cells

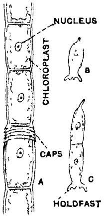


FIG 302 – *Œdogonium*. A, Part of filament, B, C, Young plants developed from zoogonidia.

§ 28. **Structure of the Cell** (Fig. 302) —The upper end of each cell is usually somewhat dilated, and frequently it shows a series of transverse ring-like markings (see § 29) The cell-wall consists chiefly of cellulose, there is little or no trace of a mucilaginous sheath Each cell contains a single large **chloroplast** consisting of a network of anastomosing protoplasmic bands lying in the parietal layer of the protoplasm. One or more **pyrenoids** are present There is a single **nucleus** lying usually near the middle of the cell

§ 29. **Cell-division.**—The way in which the growth and division of the cells are effected is peculiar and characteristic. A ring-like cushion of cellulose is formed on the inner surface of the cell-wall near the upper end of the cell (Fig 303, A) and the nucleus of the cell divides into two. The cell-wall then splits all round just outside the cellulose cushion, and the latter is stretched out so as to give rise to a membrane which is intercalated in the cell-wall (X in Fig. 303 B)

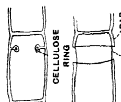


Fig 303 —*Œdogonium*. Method of cell growth (X = intercalated membrane)

The dividing wall, laid down between the two nuclei, is formed opposite the lower end of the intercalated membrane The bounding wall of the upper cell therefore consists chiefly of the intercalated membrane, but there is a portion of the old cell-wall, fitting like a cap, at the upper end of the cell, where it produces a transverse ring-like mark.

If the process is repeated the new cellulose cushion arises immediately below the previously formed ring. In this way cells frequently come to show a series of "caps" or rings at their upper ends (Fig 302, A).

§ 30. **Asexual Reproduction** (Fig 304) is effected by means of zoogonidia Any cell of the filament may function as a gonidangium and produce a *single* zoogonidium by rejuvenescence of its protoplasmic contents The **zoogonidium** is set free by a transverse split which is formed at the upper end of the gonidangium It is a comparatively large pear-shaped body Its broad posterior end contains chlorophyll, its narrow end is clear and bears a ring of **cilia.**

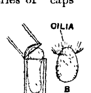


Fig 304 —*Œdogonium* A, Zoogonidium escaping, B, Zoogonidium

After a short motile period the zoogonidium settles down and attaches itself to some object by its anterior

end The cilia are withdrawn, a cell-wall is formed, and a new filament formed. The basal cell in some species remains short and blunt; in others it becomes pointed and may branch to form a root-like process of attachment

§ 31 **Sexual Reproduction** (Figs. 305, 306).—The sexual organs are *oogonia* and *antheridia* The **oogonia** are usually formed in series on a filament Any cell may become an oogonium, but most frequently it is a cell showing rings or "caps" at its upper end. The cell becomes globular or oval, and its contents are rounded off to form a single **oosphere.** The oosphere contains abundant chlorophyll, but on the side where fertilisation will be effected there is a clear "*receptive spot.*" It is not set free from the oogonium Before fertilisation either a transverse split or a pore (according to species) appears at the upper end of the oogonium and through this the spermatozoid reaches the oosphere, which it enters at the "receptive spot."

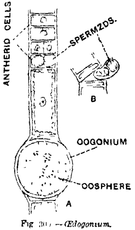


Fig. 305.—*Œdogonium.* Sexual Reproduction. (Monœcious species.)

The **antheridium** is a short cell or a series of short cells* formed by division of the cells of the filament (Fig. 305) Each antheridial cell by division of its contents gives rise to two spermatozoids, which resemble the zoogonidia, but are much smaller and contain less chlorophyll; they consist largely of nuclear matter

Many species of *Œdogonium* are monœcious In a few diœcious species the male and female plants are both large, they are called *diœcious macrandrous* species. In the great majority of the diœcious species, however, constituting

* Some regard each cell of the series as an antheridium.

nearly half of the known species, the sexual reproductive processes are highly specialised. The antheridia are produced on *dwarf* male plants, known as *nannandria*. Hence these species are called *diœcious nannandrous*

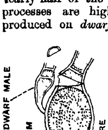


Fig. 306.—*Œdogonium*. Diœcious nannandrous species. Dwarf male on Oogonium.

In these diœcious nannandrous species special motile spores, known as **androspores** (androgonidia), are produced by the female plants in **androsporangia** (androgonidangia), which are either single cells or rows of cells resembling the antheridial cells, but rather larger. Each cell of the androgonidangium gives rise to an androgonidium intermediate in size between a zoogonidium and a spermatozoid, but resembling these. The androgonidium, after a short motile period, attaches itself to a female plant either near, or actually on, an oogonium. It there produces a "dwarf male" or *nannandrium* consisting of a basal cell, and an antheridium of one cell or a number of cells (Fig. 306). The spermatozoids produced in the antheridium are set free either by the disorganisation of the antheridial cells, or by the separation of a lid at the top.

§ 32. **Germination of the Oospore.**—The fertilised oosphere forms a cell-wall and becomes the oospore. It is at first green, but later loses its chlorophyll and becomes brown. It contains oil. Its wall is thickened and it passes through a period of rest.

It is finally liberated by the decay of the wall of the oogonium. At germination its contents, enclosed in a thin gelatinous membrane, escape and undergo division into four **zoospores** exactly resembling the zoogonidia. This is regarded as representing a rudimentary **sporophyte generation.**

The zoospores, like the zoogonidia, give rise to new plants. These are usually asexual plants, producing zoogonidia only, and as a rule they give rise to several

generations of asexual plants before the appearance of plants producing sexual organs as well as zoogonidia (see p. 463).

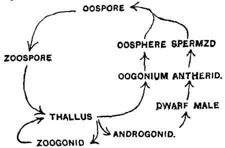


Fig 307 —*Œdogonium.*
Life-history of nannandrous species. Graphical representation

The life-history of a diœcious nannandrous species may be represented as in Fig 307.

Fucus.

§ 33. **General Appearance and Habit.**—The Phæophyceæ or Brown Algæ, to which *Fucus* belongs, are with few exceptions seaweeds. In the lower forms the sexual reproduction is isogamous; in the higher forms, heterogamous. Many of them are small and filamentous, but the group includes some of the largest forms of Algæ.

Fucus is one of the larger forms and includes several common species differing in certain minor characters When full-grown, the plant consists of a basal, branching, *root-like organ* of attachment, a straight, cylindrical *stalk-like portion*, and a dichotomously branched *membranous expansion* (Fig. 308).

The **vegetative body** is essentially thalloid, although in the organ of attachment there is a distinct indication of the differentiation of root from shoot. It should be noticed, however, that the root-process has no absorbing function and is simply a fixing organ. It is called the *disc* or *hold-fast.*

Running up the middle of each flattened lobe of the thallus is a sort of midrib, due to the thickening of the tissue in that region. In the older parts of the thallus the marginal portion dies away and leaves only the midrib This is the mode of origin of the cylindrical stalk which represents the persistent thickened midrib of the older part of the thallus A distinct stalk is not recognisable in the young plant

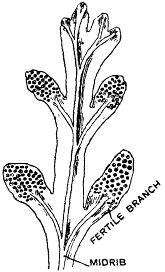


FIG. 308.—BRANCH OF FUCUS PLATYCARPUS

Fucus inhabits the zone between low and high tide-marks It is exposed at low tide, covered at high tide It is interesting to notice how well the structure of the plant is adapted to this habitat, where it is exposed to the full force of the waves. The strong fixing organ attaches the plant to rocks, etc, and prevents it from being washed away. It is preserved from injury by the pliant nature of its stalk, and the yielding, flattened character of its branches Some species (*F. vesiculosus*) are rendered still more buoyant by the development of **air-bladders**—hollow dilatations of the thallus filled with air. The plant is saved from excessive desiccation, when exposed between tides, by the mucilaginous character of its tissues.

If we examine the apices of the branches at certain periods it will be found that they are covered with small papillæ, and are more or less swollen (Fig 308). These papillæ mark the position of internal flask-shaped cavities, called **conceptacles,** in which the sexual organs are developed, and hence protected by being enclosed in the tissue of the thallus.

In some species, e.g. *F. serratus*, small dots are found scattered over the thallus These mark the position of pits in which hairs are developed, and which may be regarded as barren conceptacles. They have been called cryptostomata.

§ 34. **Structure and Growth of the Thallus.**—A section, passing through both surfaces and taken at any part of the thallus, will show that a central or **medullary region** of tissue can be distinguished from an outer or **cortical region** on each side (Fig. 309).

The outermost layer of the cortex (**outer limiting layer**) resembles an epidermis, but it is quite different

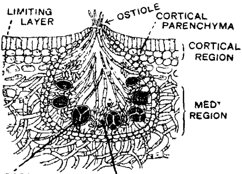


Fig 309 —*Fucus Platycarpus.*
(Transverse section, through a conceptacle.)

from a true epidermis. Its cells are *meristematic* and by division give rise to new cortical cells This is the assimilating region of the thallus; the cells contain chloroplasts, in which the green colour of the chlorophyll is masked by the brown colouring matter phycophæin.* The subjacent cells are parenchymatous, with distinctly pitted walls; they constitute the **cortical parenchyma.** It is the storage region of the thallus. No starch is formed in *Fucus.* The product of metabolism is a carbohydrate

* However, see footnote, p 511.

somewhat resembling starch, but it is not stained blue by iodine.

The medulla consists of an interlacing network of filaments or hyphæ embedded in a clear mucilaginous matrix. The filaments are divided at intervals by septa. It is a tissue in which the outer layers of the cell-walls have become mucilaginous. The rows of cells still enclosed in the inner layers of their cell-walls constitute the filaments. The medulla is essentially the conducting tissue of the plant. The cross-walls between the segments of the hyphæ are perforated like sieve-plates, and in *Laminaria*, a large Alga allied to *Fucus*, distinct sieve-tubes are developed.

In the older parts of the thallus there is a similar structure, but the outer limiting layer is lost, and the cortical parenchyma by meristematic activity gives rise to secondary increase in thickness. This can be observed in the region of the stalk. The hyphæ of the medullary region also increase in number.

At each growing point of the thallus there is a group of four or five **initial cells**, each of which assumes the form of a four-sided truncated pyramid. The segments from the bases of these cells form medullary hyphæ, those from the sides form mainly cortex. At each branching the apical cells separate into two similar groups (true dichotomy) *

§ 35. **Reproduction.**—There is no special method of asexual reproduction in *Fucus*, but sometimes adventitious branches, formed at the base of the thallus by the activity of the cortical meristem, may be separated off and form new plants. There is abundant **sexual reproduction.** The plant belongs to the sporophytic generation, having the double number of chromosomes in its cells. Reduction of chromosomes occurs during the formation of the sexual cells, which are therefore gametophytic. The sporophytic phase begins again with the fertilised egg. In contrast with *Spirogyra*, the gametophyte is here much reduced. The sexual organs are contained in the conceptacles men-

* According to some the group of initial cells is derived by division from a single apical cell.

tioned above. Each **conceptacle** (Fig 309) opens on the surface of the thallus by a minute aperture called the **ostiole.** Numerous multicellular **hairs** are developed from the cells lining the conceptacles. Many of these form *paraphyses*; others bear the sexual organs.

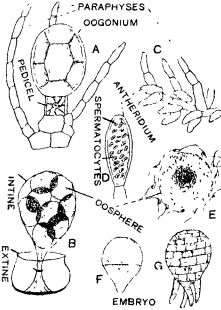


Fig 310 —*Fucus vesiculosus*
A—D Sexual organs, E, Fertilisation, F, G, Embryo.

In the development of a conceptacle one or several superficial cells of the thallus cease to grow and become disorganised The surrounding tissue grows vigorously, and soon encloses a flask-shaped cavity.

§ 36. **The Sexual Organs** (Figs 309, 310) are antheridia and oogonia. The **antheridia** are borne in clusters, and represent the finer branches of much-branched hairs.

Each antheridium is developed from a single cell. When fully formed it is a small, oval, orange-coloured sac, the wall of which consists of two thin membranes called the *intine* and *exine*. The contents have undergone division to form a large number of small spermatocytes from which the biciliate **spermatozoids** are developed. The cilia are developed laterally, and each spermatozoid has an orange-coloured **chromatophore.**

The **oogonium** is a much larger, dark-coloured structure. It also is developed from a single cell. It is borne on a short unicellular pedicel representing an abbreviated hair. Its wall also consists of *intine* and *exine* and its contents divide to form eight **oospheres.**

The plants are usually *diœcious*, e g. *F vesiculosus*, recognised by its bladders, and *F serratus*, recognised by its serrate margin; but in *F platycarpus* (Figs. 308, 309) the sexual organs are borne on the same plant and in the same conceptacle.

§ 37. **Fertilisation** (Fig 310, E).—When the spermatozoids and oospheres are ripe, the antheridia and oogonia become detached. The exine is ruptured (B), and the contents, enclosed in the intine, move towards the ostiole. This generally takes place when the plants are exposed at low tide. The hairs of the conceptacle secrete a mucilaginous substance. This oozes out of the ostiole, carrying with it the sacs of spermatozoids and oospheres. When the tide rises again the intine is ruptured, and the spermatozoids *and oospheres* are set free into the water. Spermatozoids cluster round each oosphere, which is thereby caused to rotate. Finally, one spermatozoid enters and its nucleus fuses with that of the oosphere. The resulting zygote is the **oospore.**

§ 38. **Germination of the Oospore** (Fig 310, F, G) —Without any resting stage, germination takes place. The oospore becomes pear-shaped, and is divided by a wall into a pointed basal cell and a rounded apical cell. The basal cell sends out a number of *rhizoids* which fix the young plant and become wefted together to form the root-disc;

the upper cell, by further division, gradually develops into the thallus. There is no alternation of generations

§ 39. **Differentiation of Sex**—In connection with the life-history of *Sphærella* we recognised the probable origin of gametes and the evolution of sexuality. In *Sphærella*, however, the gametes are similar, and, further, sexuality is not *completely* established. In *Ectocarpus*, a brown Alga, the gametes are also similar and sexuality is imperfect, but some of the gametes are less active and come to rest sooner than others In some species of *Ectocarpus*, and in *Cutleria* (another brown Alga), the gametes are of two sizes. The larger ones are less active and come to rest sooner than the more active smaller ones which fuse with them.

Here we have a series of Algal types which enable us to trace the probable evolution of sexual differentiation. This evolution undoubtedly took place along different lines. The larger gametes are female Their larger size and more passive character probably originated in a more abundant storage of food-material, making better provision for the embryo plant. We have the next stage in *Fucus*. Here the gametes are fully differentiated and the ovum is not ciliated But *both gametes are set free into the water*. This is a striking feature in the life-history of the Fucaceæ. The next step in the evolution is to the stage where the female gamete is retained in the female organ.

§ 40. **Relationship of the Algæ to the Higher Plants.**—The Algæ are an interesting group, supplying many facts which help towards the elucidation of important problems Amongst them there are many divergent lines of evolution Along most of these lines we recognise a gradual transition from isogamous to heterogamous reproduction There can be no doubt that the primitive ancestors of the Bryophyta and Pteridophyta were evolved from primitive Algal forms; but here the gap is too wide for us to bridge over.

CHAPTER XXII.

FUNGI AND BACTERIA.

§ 1. The Fungi constitute the second important Class into which the Thallophyta are subdivided. They are readily distinguished from the Algæ by the want of chlorophyll; chromatophores and starch also are entirely wanting. This *by itself* would not be a sufficient reason for separating the two classes. If this were all we might, with equal reason, separate those few Flowering Plants which have no chlorophyll from the rest. The Fungi, however, as a whole, are further distinguished by special characters in their structure, development, and life-history.

§ 2. **The Mycelium.**—The typical vegetative structure of the Fungi is a filamentous and much-branched thallus called a *mycelium* The filaments or threads of which the mycelium consists are called **hyphæ.** Sometimes we find more massive structures, more especially in the parts bearing the reproductive organs. When we examine these, however, we find that they consist of hyphæ woven together so as to form **a false tissue**, *i.e.* a tissue formed, not by the division of cells all originally connected with each other (true tissue), but by the interweaving of separate hyphæ. Occasionally, in very degenerate forms like yeast, the plant consists of separate cells.

The mycelium (or its hyphæ) may be septate or non-septate. In most cases it is cœnocytic; even where it is septate the different segments usually contain several nuclei, and are hence cœnocytic cells. The cell-walls of most Fungi do not consist of cellulose, but of chitin, a substance forming the protective coats of insects and crustaceans.

§ 3. **Nutrition.**—The nutrition of fungi is quite different from that of ordinary green plants. Having no chlorophyll they can make no use of the carbon dioxide of the atmosphere. They derive their carbonaceous food-material from complex organic compounds which they obtain from external sources This also, to a large extent, applies to the absorption of nitrogen. Fungi, however, can assimilate comparatively simple compounds of nitrogen; but they prefer ammonium compounds, *e.g.* ammonium tartrate, to nitrates. Altogether their food-materials are less complex than those of animals.

§ 4. **Mode of Life.**—Fungi may live either as parasites or as saprophytes. Some are not confined to one mode of life, but may live as parasites or as saprophytes, according to circumstances. In a parasitic fungus the hyphæ may penetrate the living cells of the host, or simply ramify between the cells The power of penetrating and disorganising cell-walls which such hyphæ frequently possess is due to the secretion of a ferment which acts on cellulose The hyphæ of a saprophyte ramify through decaying organic substance or grow immersed in organic solutions. The whole of the mycelium may be absorptive, but some parasites, whose hyphæ ramify between the cells of the host, develop special absorbing organs (*haustoria*) which penetrate the cell-walls and enter the cells.

§ 5 **Reproduction and Life-history.**—There can be no doubt that the Fungi were originally derived from Algal forms—that the ancestral types were, in fact, simply Algæ which assumed a dependent mode of life, and lost their chlorophyll. As supporting this view, we find that in the lower forms of Fungi, the Phycomycetes, to which *Mucor* and *Pythium* belong, there is a close resemblance to certain green Algæ like *Vaucheria* Their reproductive organs are very similar, and frequently also their general structure presents a close resemblance The other groups of Fungi, the Ascomycetes and Basidiomycetes, constituting the class called Eumycetes or Mycomycetes, diverge widely from the Algæ and present very special

characters. The Ascomycetes, however, show some striking resemblances to the Red Algæ, and were probably derived from the same ancestral stock.

The occurrence of functional sexual organs in some of the Ascomycetes has now been established; but in most of the Ascomycetes and Basidiomycetes the sexual processes have undergone a marked reduction. This is another mark of that degeneracy among the Fungi which is otherwise indicated by their low organisation; this degeneracy is to be ascribed to their mode of life.

Amongst the Fungi we recognise that there has been a gradual adaptation to aerial conditions, becoming very perfect in the higher groups Evidence of this is found in the fact that, even in the group which lies nearest to the Algæ, the gametes are not ciliated (except in one small family), and that in the other groups the "spores" or **gonidia** are eminently adapted for transport through the air When the gonidia are cut off from the end of a hypha by a process resembling budding they are called *conidia*.

The types whose structure and life-history we now proceed to describe will serve to illustrate most of the above points.

MUCOR

§ 6. **Structure and Mode of Life.**—*Mucor* is one of the commonest of those Fungi which are called "moulds." In its mode of life it is a saprophyte, and grows on many different kinds of organic substance. A growth of it can readily be obtained if fresh horse-dung, or bread which has been soaked in water, is kept under cover for four or five days at a moderate temperature. It makes its appearance in the form of little white patches, which gradually spread and unite. The commonest species are *M. mucedo* and *M. stolonifer*.

The **mycelium** (Fig 311) is copiously branched. It ramifies in the organic substance on which the fungus is growing, and absorbs nourishment from it The branches, or **hyphæ**, get finer and finer the deeper they pass into the substratum The structure of the mycelium can readily be made out if a portion of it be teased out in water on a

slide, and examined under the microscope. The finely granular protoplasm contains small vacuoles and oil-globules. With special methods of preparation the presence of numerous small nuclei can be demonstrated. In an actively growing mycelium there are no septa, although these may occasionally be found in old growths. The mycelium, therefore, does not consist of definite cells, but is a cœnocyte.

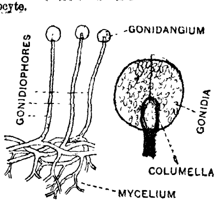


Fig. 311 —*Mucor.*
A, A portion of a mycelium bearing gonidiophores. B, A single gonidangium.

§ 7. **Asexual Reproduction** (Fig. 311).—This is effected by means of small oval gonidia. If a growth of *Mucor* be observed, rather stout aerial branches will be found springing from the surface of the mycelium. Each bears at its tip a spherical sac, which is a gonidangium (p. 463). The gonidangium is formed simply by the swelling of the upper end of the aerial branch. It is cut off from the lower portion, the **gonidiophore**, by a distinct septum, which afterwards, during further development, protrudes into the gonidangium to form a structure called the **columella**. As the gonidangium ripens it becomes black. Its wall is studded with spicules of calcium oxalate.

The gonidia are developed inside the gonidangium by

division of the protoplasmic contents; they are multinucleate. The part of the protoplasmic contents which is not used in their formation gives rise to a mucilaginous substance, which later, by absorption of water, brings about the bursting of the gonidangium. Each gonidium, when set free, puts out a germ-tube and forms a new mycelium.

The gonidangia and gonidia are also called sporangia and spores (or endospores) respectively (see p. 512). The gonidia are not called conidia here, as they are not formed by abstriction from a hypha (see p. 539).

§ 8 **Sexual Reproduction** (Fig 312).—Sexual organs may be formed in *Mucor*, although not so frequently as in some closely-allied forms. Their development seems to depend on external conditions.

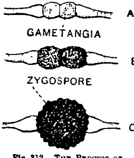


Fig 312 —The Process of Conjugation in Mucor.

The sexual method of reproduction is isogamous, and consists in the conjugation of undifferentiated motionless gametes (cf. *Spirogyra*), leading to the formation of a zygospore In the process two mycelial branches, the **gametophores**, approach each other, and their terminal portions are cut off by the formation of septa to form **gametangia**, whose undifferentiated protoplastic contents constitute the **gametes**. The latter are multinucleate, and for this reason have been called *cœnogametes*.

The gametangia meet, and owing to gradual absorption of the walls at the point of contact, the two gametes come together, and fuse with each other. The structure thus formed is the young **zygospore**. When fully developed it is black, and its wall consists of two layers, a rough cuticularised exosporium and a delicate endosporium.

The mycelia of some species of *Mucor* show a physiological differentiation into two *strains* or *races*, conjugation occurring only between gametes derived from two mycelia

of opposite strains. These species have been called *heterothallic*. In other species, which are *homothallic*, the mycelium produces both kinds of gametes, so that zygospores may be obtained from one and the same mycelium. Occasionally a slight difference in size may be observed in the two gametes in *Mucor*, hinting at a morphological differentiation of sex.

§ 9. **Germination of the Zygospore** (Fig. 313).—After a period of rest the zygospore germinates. The exosporium is ruptured, and the endosporium grows out to form a simple or slightly branched tube called the **promycelium**. This bears at its apex a single spherical sporangium which resembles in all respects the gonidangium described above. Each of the spores formed inside it on germination produces a normal mycelium.

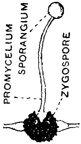


Fig 313 —GERMINATION OF THE ZYGOSPORE OF MUCOR

Some botanists regard the promycelium as a rudimentary sporophyte. Others regard the promycelium as simply a reduced or rudimentary mycelium, and do not admit that the alternation found here is at all comparable with the alternation found in higher types.

The gametes may develop without conjugation. Either fusion fails to take place or the gametes are produced singly. They give rise to thick-walled cells, which germinate like zygospores, and are called **azygospores** (see p. 473).

§ 10. **The Torula Condition.**—If the mycelium of *Mucor* is immersed in a nutritive solution, it may break up, by the formation of septa, into chains of cells. These cells are sometimes thick-walled, and are simply resting-cells (chlamydospores or chlamydogonidia), which, under normal conditions, would produce new mycelia. Frequently, however, they are thin-walled (oidium cells). In this case they separate from each other, and are not only capable of

budding or sprouting like yeast-cells, but, like yeast-cells, are also able to produce alcoholic fermentation in a saccharine fluid. This is known as the "torula condition" of *Mucor*.

§ 11. *Mucor* belongs to the group of Phycomycetes known as Zygomycetes, in which there is isogamous sexual reproduction.

PYTHIUM.

§ 12. **Structure and Mode of Life.**—If large numbers of cress-seedlings (*Lepidium sativum*) are grown together under very moist conditions, it is found that they become "diseased" They fall over, turn pale and then brown, and finally begin to rot. The disease begins at certain

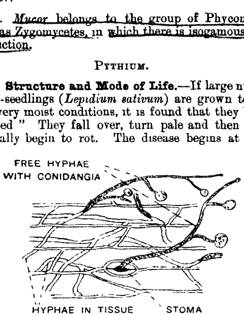


Fig 314 — PYTHIUM
Epidermis of a plant attacked by the fungus.

points, and spreads in circles. It is spoken of as the "damping off" of seedlings, and is caused by the attack of a fungus called *Pythium de Baryanum*, one of the commonest species of *Pythium*.

The fungus attacks the seedling near the base, and begins to eat into its tissues, penetrating upwards into the stem and downwards into the root. The disease can be stopped at an early stage by admitting abundant light and air, for *Pythium* can live only under moist conditions. If

the moist conditions are maintained, the hyphae of the fungus extend from one seedling to another until they are all reduced to a blackened rotting mass, covered by dense white felts of mycelia like spider's web. The fungus, beginning as a parasite, continues to live as a saprophyte. Other species of *Pythium* attack seedlings in the same way; some live normally as saprophytes

The **mycelium** of *Pythium* (Fig 314) is a much-branched, non-septate cœnocyte (cf. *Mucor* and *Vaucheria*) Its protoplasm contains numerous small nuclei and oil-globules The hyphae may eat right through the cells of the host or ramify between them.

§ 13. **Asexual Reproduction** (Fig 314).—If a diseased seedling is placed in a watch-glass in water and kept under observation, it will be found that the ends of some of the hyphae, which grow out from the surface of the plant, or of small branches of these, swell up and become globular. These globular swellings are cut off by distinct septa. They are asexual reproductive organs. They produce new mycelia in two ways, according to the conditions under which they are developed.

Sometimes, if there is scarcity of water, they function as "spores" or **conidia**, and each without being set free sends out a germ-tube which grows into a mycelium directly. At other times, when there is abundance of water, they function as **gonidangia** (also called zoosporangia). Each (Fig. 315, a-e) develops a little protuberance which expands to form a round

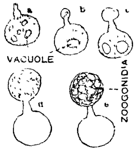


Fig 315.—GONIDANGIUM OF PYTHIUM
Stages in the production of zoogonidia.

thin-walled vesicle into which the protoplasmic contents pass. These divide into a number (9 or 10) of **zoogonidia**, which are set free by the rupture of the wall of the vesicle. The zoogonidium is a very minute, colourless body with

two cilia After moving about for some time it comes to rest, withdraws its cilia, rounds itself off, and forms an investing wall. A hypha is then sent out, which makes its way into another seedling, either by boring through the wall of an epidermal cell or by means of a stoma.

The production of zoogonidia is a distinct resemblance to what we find in the Algae, but there is an *indication* of adaptation to aerial conditions in the fact that the reproductive bodies may germinate directly.

§ 14. **Sexual Reproduction** (Fig. 316).—The female organ is an **oogonium.** It may be formed on the end of a hypha (terminal) or on the course of a hypha (intercalary), either outside the seedling or in the tissues of the seedling It arises as a globular swelling of the hypha, and bears a close resemblance to the asexual reproductive organ. It is cut off by a septum from the rest of the hypha. At first the protoplasmic contents have many nuclei, but soon a central region containing one nucleus, constituting the **oosphere,** is marked off from a peripheral region, called the **periplasm,** containing the other nuclei.

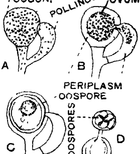


Fig 316 —SEXUAL REPRODUCTION IN PYTHIUM.
B, Fertilisation, D, Germination of oospore.

The male organ, called the **pollinodium,** is developed on a branch which arises either on the same hypha as the oogonium, or on another hypha It is separated off by a distinct septum, and its protoplasmic contents are differentiated into a central portion, the **male gamete,** and a peripheral *periplasm*. The male gamete has no cilia, and for this reason the male organ is usually called a pollinodium and not an antheridium. By some, however, it is called the antheridium.

The pollinodium is more or less club-shaped. It applies

itself closely to the oogonium, and develops a tubular process, the **fertilisation-tube**, which pierces the wall of the oogonium and carries the male gamete to the ovum. This process can be readily observed in *Pythium*. The fertilised ovum forms a thick wall and becomes the **oospore.** The outer layer of the wall is formed from the periplasm.

The sexual organs and oospores are produced after the asexual organs, when the conditions for rapid growth and reproduction by asexual methods are becoming unfavourable. The oospores are essentially resting spores. They remain inactive during the winter and germinate in the following spring. This is why seedlings grown on the same ground as seedlings attacked the previous year are so liable to the disease.

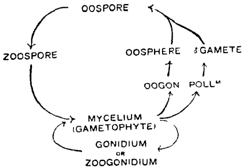


Fig 317 —Graphical Life history of Pythium.

If the conditions are favourable the oospore sends out a hypha which directly develops into a mycelium, if unfavourable, the oospore either forms a number of small **zoospores** directly from its protoplasm, or sends out a little tube or hypha, called a **promycelium,** in which zoospores are developed (Fig. 316, D). The zoospores closely resemble the zoogonidia and germinate in the same way. The promycelium has been considered to represent a very rudimentary sporophyte. Where it is not developed the oospore in itself, or together with the zoospores it produces, may be supposed to represent the sporophyte (Fig 317).

§ 15. *Pythium* belongs to the group of Phycomycetes known as Oomycetes, in which the sexual reproduction is heterogamous. The close resemblance between the structure of the mycelium and the reproductive organs of *Pythium*, and the thallus and reproductive organs of *Vaucheria* should be carefully noticed.

EUROTIUM

§ 16. **Habit and Structure.**—*Eurotium* is a saprophyte. It lives on decomposing organic substance. It is frequently found on the surface of mouldy bread, damp fruit and vegetables, preserved fruit, etc, and belongs to the miscellaneous group of Fungi known as moulds, which form filamentous growths on the substances on which they live. If a piece of dry, stale bread be kept under a bell-jar, one of the commonest species, *Eurotium Aspergillus-glaucus*, a green mould, will be found. At first, before the reproductive bodies are developed, the mould is white; but when it enters on the reproductive stage it assumes a greenish colour.

The mycelium (Fig 318) consists of a tangled mass of hyphæ ramifying in and on the surface of the nutrient substratum. It is much branched, and the hyphæ are divided at intervals by transverse septa Each segment of a hypha contains a mass of granular vacuolated protoplasm, with several nuclei and oil-globules. The structure is cœnocytic. Starch and plastids are wanting. The hyphæ which ramify beneath the surface absorb nutrient organic substance.

§ 17 **Asexual Reproduction** (Fig. 318).—From the mycelium numerous straight and, as a rule, non-septate branches pass up into the air. Each is given off from a hypha, usually at a point immediately behind a septum. These branches bear the **conidia** (gonidia), and are therefore called **conidiophores** (gonidiophores). The head of each conidiophore swells up and becomes spherical. On this spherical head arise a large number of peg-like outgrowths called **sterigmata.** From the apex of each

sterigma as it elongates conidia are separated by abstriction one after the other. In this way rows or chains of conidia are formed on the sterigmata; the oldest conidia are at the apex of each row.

The conidia are small oval bodies with a greenish colour and more or less spiny surface Their protoplasm contains several nuclei and oil-globules, and they have two coats, *exosporium* and *endosporium* These conidia are produced in enormous quantities, and are very readily carried through the air. It is because they are always present in the atmosphere that decaying substances so readily become infected with the fungus. On reaching a suitable substratum they germinate in the usual way, and produce new mycelia directly. They will germinate very readily in a *weak* decoction of plum juice.

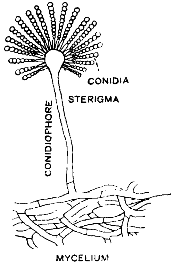


Fig 3 o.—EUROTIUM MYCELIUM AND CONIDIOPHORE

§ 18 **Sexual Reproduction** (Fig. 319) —In *Eurotium* the same mycelium which has produced conidia eventually bears sexual organs. The female organ is called an **archicarp**. It differs from the female organs we have already become familiar with in that its protoplasm is not rounded off to form an ovum. The male organ is a **pollinodium.**

In the development of the archicarp the end of a hypha becomes coiled, at first loosely, but later very closely This tightly-packed spiral organ, consisting of four or

five coils, is the archicarp. In *Eurotium* it is at first non-septate, and its protoplasm is multinucleate. The apical portion is called the trichogyne; the lower coiled portion, the carpogonium. Several slender branches arise from the hypha beneath the archicarp. One of these develops faster

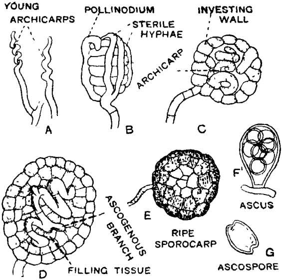


Fig. 319.—EUROTIUM DEVELOPMENT OF SPOROCARP AND ASCOSPORES.

than the others, and arches over to the apex of the archicarp. It is the pollinodium, like the archicarp, it is non-septate and multinucleate.

Fertilisation is effected by the contents of the pollinodium passing over into the archicarp. The actual process of transference, after having been long and carefully looked for, has now been described by several observers. The other branches arising below the archicarp are sterile. At first few in number, they are afterwards numerously developed. They wrap round the archicarp, and, by inter-

weaving and septation, give rise to a false tissue (pseudoparenchyma), completely enclosing it. This false tissue sends in hyphal branches between the coils of the archicarp, and thus gives rise to a "filling tissue" which separates the coils.

The fertilised archicarp becomes septate and develops small outgrowths, the *ascogenous branches*, which penetrate into the false tissue. The ends of these outgrowths are cut off by septa and form unicellular sporangia called **asci.** The young ascus has at first two nuclei These fuse together, and then, by a process of free cell-formation, eight **ascospores** are formed inside the ascus. The peripheral protoplasm of the ascus (epiplasm) is not used up in the formation of ascospores. It contains a large quantity of a carbohydrate called glycogen, serving for the nourishment of the spores. During the development of the asci the whole of the central "filling tissue" is disorganised Thus from the archicarp and the investing sterile hyphæ, a **sporocarp** has been formed.

The wall of the sporocarp consists of small-celled pseudoparenchyma, and encloses a number of eight-spored oval asci. It is also spoken of as an *ascocarp*. In the ripening of the sporocarp only the outermost layer of the wall persists; its cells become dry and firm and covered with an oily secretion, which gives the sporocarp a yellow colour. The asci are disorganised, and the ascospores are eventually liberated by the bursting of the wall of the sporocarp. The ascospore, which was oval when young, is biconvex when fully developed. In germination the exosporium is ruptured; the endosporium grows out and directly produces a mycelium.

§ 19. **Eurotium** is a type of the large group of Fungi called **Ascomycetes,** which are characterised by the production of asci and ascospores. It was formerly a disputed point whether the archicarp and pollinodium were really sexual organs Some regarded the archicarp simply as an organ producing another kind of asexual "spore" or gonidium, and the pollinodium as one of the sterile hyphæ According to this view there was no indication

of an alternation of generations, and Eurotium exhibited a form of *polymorphism* quite different from that exhibited in the alternation of gametophyte and sporophyte—namely the production at different stages of two kinds of asexual organs. Now that the archicarp and pollinodium are known to be sexual organs we may regard the life-history as showing an indication of an alternation, in which the fertilised carpogonium and the ascogenous hyphae represent the sporophyte. The gametophyte begins with the ascospores, during the formation of which reduction takes place.

§ 20 **Penicillium glaucum** is a blue mould very similar in habit and structure to Eurotium. The apex of each conidiophore, instead of being globular, divides into a number of finger-like processes bearing the sterigmata. In Penicillium sporocarps are developed only in special circumstances—namely, when free access of light and air is prevented The conidia of this fungus, if grown in a saccharine solution, under certain conditions, give rise, not to a filamentous mycelium, but to isolated cells resembling yeast This is the **torula condition** (cf *Mucor*, p 493) Like yeast, it excites alcoholic fermentation.

CLAVICEPS PURPUREA (ERGOT OF RYE, ETC.).

§ 21. **General Life-history.**—The life-history of this fungus shows three well-marked stages or phases, and affords an illustration of the polymorphism which is so common amongst Fungi.

(1) The **Sphacelia** or **"Honey-dew" stage** is found on various cereals and grasses. It has been most carefully studied in the case of Rye (*Secale cereale*), but it also occurs on Barley, Wheat, etc , and on some of the grasses commonly found on roadsides, in meadows, and in waste places (e g. *Lolium perenne*). It is the active parasitic stage in which the fungus attacks the developing pistil, and forms a mycelium which grows vigorously and reproduces itself by means of conidia (Fig. 289).

(2) The **Sclerotium stage** is the resting or winter stage. In autumn, the *Sphacelia* forms a hard, slightly curved body, of a dark purple or black colour, which protrudes from between the paleæ of the flower, and may

attain the length of an inch or even more (Fig. 322, A). It falls to the ground and undergoes no change till the following spring. It was to this body that the name ergot was first given in reference to its shape (from O. Fr. *argot*, a cock's spur). Hard resting bodies of this kind are formed by many fungi and are called **sclerotia**

(3) The **Ascospore stage.**—The sclerotium or ergot eventually produces a number of club-headed structures, called **stromata** (Fig. 322, B), in which asci and ascospores are developed. From these the Sphacelia form again arises.

At first the connection between these three stages was not recognised. They were regarded as distinct fungi and received the generic names *Sphacelia*, *Sclerotium*, and *Claviceps* * respectively. The last is now taken as the generic name of the fungus in all its forms.

§ 22. The **Sphacelia Stage** (Figs. 320, 321).—The ascospores, which are peculiar in being very slender and thread-like (Fig 325, B), are liberated just when the flowers of the host plants are appearing. They are carried to the flowers by wind and there germinate. In the process of germination little swellings appear on the ascospore, and at these points the germ-tubes are developed They pierce through the epidermis and make their way into the tissue at the base of the young ovary.

The **mycelium** which is rapidly developed consists of septate hyphæ It not only ramifies in the tissue of the ovary, but also, after a time, spreads over its surface and envelops the greater part of it with a dense white covering of interwoven hyphæ, showing numerous folds and convolutions This investment is the **conidiophore**. The free ends of the hyphæ become slightly swollen, and form **sterigmata** from which small oval **conidia** are successively abstricted (Fig 320).

The conidia are developed in great numbers, and are embedded in a sweet and somewhat viscid fluid which is formed by the disorganisation of the outer layers of the walls of both hyphæ and conidia. This fluid is called

* Latin *clava*, a club.

"**honey-dew**" and its appearance on rye and other crops is a source of anxiety to the farmer. Flies and other

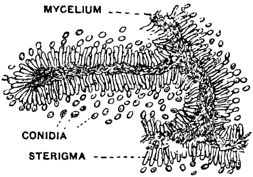


Fig. 320.—CLAVICEPS (SPHACELIA STAGE) Section of Conidiophore.

insects are fond of it. They are attracted to it by its odour, and by their agency the infection is spread to other plants. A conidium carried in this way to another flower sends out a germ-tube which pierces the base of the ovary and produces another mycelium.

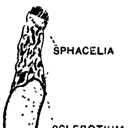


Fig 321 —CLAVICEPS. Vertical section through developing sclerotium.

§ 23. **The Sclerotium Stage** (Figs 321-323).—When the growth of the mycelium has continued for a considerable time, the mass of interwoven hyphæ at the base of the shrivelled pistil becomes densely compacted, and forms a false tissue which is the beginning of the sclerotium. The outer layers of this tissue become dark-coloured and growth now goes on actively in this region The sclerotium rapidly elongates and assumes its curved horn-like shape. As it does so it

bears at its apex the remains of the *Sphacelia* and the pistil (Fig 321), and finally these are thrown off

The sclerotium or ergot is fully formed just when the grain ripens. It then protrudes from between the paleæ, but is easily detached. Unless the crop is harvested early, it falls to the ground and there remains in a dormant condition till the following spring (Fig. 322, A).

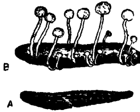


Fig 322 — CLAVICEPS.
A, Sclerotium, resting stage, B, Sclerotium with stromata.



Fig 323 —CLAVICEPS.
Transverse section of germinating sclerotium showing a developing stroma.

If a transverse section of the sclerotium be taken (Fig. 323) it is found to consist of a dense pseudoparenchyma formed of fine united hyphæ. The outline of the section is somewhat irregular and is interrupted in places by fissures or cracks. The outer layers are very dark-coloured. The cells of the central tissue are laden with oil, and also contain an alkaloid, called *ergotin*, and other poisonous substances, to which the peculiar properties of ergot are due

§ 24. The **Ascospore Stage.**—In spring or early summer the sclerotia begin to develop their stromata. The process can be readily observed if at this time some of them (in good condition) be kept half buried in damp clean sand under a bell-jar. The first sign of development (it may not be till after the lapse of several weeks) is the appearance of a number of little swellings on the surface and sides of the sclerotium. Then the dark-coloured outer layer is gradually ruptured, and the light-coloured heads of the stromata protrude (Fig. 323) The development of

each stroma is due to the outgrowth of a tuft of hyphæ from the light-coloured inner tissue of the sclerotium.

Each stroma consists, when fully developed, of a light coloured purplish stalk, an inch or more in length, and a rounded head of a light brown or orange colour (Fig. 322, B) As in the case of the sclerotium, the hyphæ of the stroma are closely interwoven and united, and form a false tissue. The head is covered with minute papillæ, on

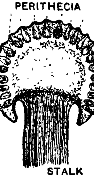


Fig 324 —CLAVICEPS
Vertical section through a stroma, showing the perithecia

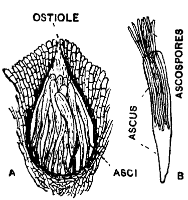


Fig 325 —CLAVICEPS.
A, Section through a perithecium, showing the asci, B, A single ascus, ascospores escaping

which are situated the openings or **ostioles** of numerous flask-shaped cavities, called **perithecia**, which lie in the peripheral tissue of the head. These perithecia can be readily seen in a vertical section of a stroma (Fig. 324).

From the cells in the floor of each perithecium are developed a number of elongated club-shaped **asci**, which project upwards towards the ostiole (Fig. 325, A). The contents of each ascus divide to form from six to eight thread-like **ascospores** (Fig. 325, B). When the asci are ripe they burst. The ascospores escape through the ostioles, and some of them, carried as already described to the young flowers of a grass, produce the *Sphacelia* again.

§ 25. **Notes on the Life-history.**—Like *Eurotium* and *Penicillium*, *Claviceps* belongs to the Ascomycetes. It is, however, placed in a different division of that class. The classification is based on the character of the sporocarp or ascocarp (p. 550). In *Claviceps* it is a perithecium, in *Eurotium*, a *cleistocarp*, that is, a closed case.

The life-history of *Claviceps* is more complicated than that of *Eurotium*, owing to polymorphism. The mycelium of *Eurotium*, after a period of asexual reproduction by conidia, produces sexual organs, and is therefore the gametophyte. What probably corresponds to the gametophyte in *Claviceps* is represented by the three forms or

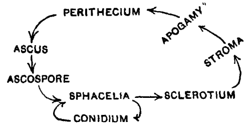


Fig 326 —Claviceps.
Graphical representation of life history

stages described above. Definite sexual organs have not, however, been hitherto discovered, and it is *possible* that the perithecia are produced apogamously. A graphical representation of the life-history is given in Fig. 326.

The life-history is also interesting from the fact that it exhibits the phenomenon known as **Lipoxeny**, that is the desertion or abandonment of host (Gr. λιπειν, to abandon, ξενος, host). The Sphacelia form, as we have seen, is parasitic on Rye and other grasses, but the fungus then deserts its host, and the resting stage is passed on the ground.

The fungus in all its forms shows remarkable adaptation to the conditions of its existence. The abundant production of conidia and the method of their distribution

(cf. insect-pollination in flowers) provide for the rapid spread of the active Sphacelia form. The sclerotium is developed and falls to the ground in time to prevent its being removed with the crop. The ascospores are produced just when the grass flowers appear, and by position and form are adapted for wind transport.

SACCHAROMYCES (= YEAST).

§ 26 **Habit and Structure.**—This is the fungus which is the exciting cause of alcoholic fermentation in saccharine solutions. *S. cerevisiæ* is the beer-yeast (brewer's yeast); *S. ellipsoideus* is the species which sets up fermentation in grape-juice in the manufacture of wine The yeast-plant is a saprophyte, and thrives best in saccharine solutions containing in addition small quantities of nitrogen- and sulphur-compounds.

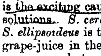


FIG 327.—YEAST-CELLS, SHOWING PULLULATION.

The mycelium is not, as in most of the other Fungi, a branched filamentous structure, but consists of isolated cells or groups of cells (Fig 327). Each cell is more or less oval, sometimes almost spherical, and contains granular protoplasm, a central vacuole, and a number of oil-globules. Each cell has also a single nucleus which can be seen by special methods of staining.

§ 27. **Vegetative Reproduction.**—The common method of reproduction is by vegetative budding. If yeast-cells in an active state of growth are examined, it is found that each gives rise to a tiny outgrowth which gradually increases in size, and is finally cut off as a separate yeast-cell. This process is known as **pullulation** or **gemmation** (Fig 327). It differs from ordinary cell-division (of which it may be regarded as a modification) only in that a cell is not directly divided into two daughter-cells, but that there is a gradual growth of a daughter-cell on the parent-cell. The daughter-cells, before being separated off, may repeat the process, and thus we have the formation of cell-groups.

§ 28. **Spore-Reproduction.**—This is met with only under unfavourable conditions, more especially when there is an insufficiency of food-material, e.g when yeast-cells are grown on the cut surface of a potato, or on moist plates of plaster-of-Paris, or left in a neglected condition in a jar. In these circumstances the process of pullulation ceases, and certain of the yeast-cells become larger and form sporangia. The nucleus of each sporangium usually divides into four nuclei. The protoplasm aggregates around each of these, and four spores are formed, each with a firm, stout wall. In some cases eight spores, or less than four may be formed. They must be considered as resting spores specially developed to cope with unfavourable conditions of existence When they germinate, on the return of favourable conditions, the outer coat of the spore is burst, and the process of pullulation begins.

The spores are developed in exactly the same way as the ascospores of the Ascomycetes. In both cases they are formed by free-cell formation, the peripheral layer of protoplasm of the sporangium not being utilised (§ 18). We have also seen that in some Ascomycetes, e g. *Penicillium glaucum* (§ 20), the yeast or torula condition is met with in certain circumstances. On these facts is based the view that the spores of the yeast are *ascospores*, and the cell (sporangium) in which they are developed an *ascus*; and that the sporangia and spores of the yeast represent in a rudimentary form a sporophyte apogamously developed. According to this view Saccharomyces is a very degraded Ascomycete in which the torula condition has become fixed.

In a few species of *Saccharomyces* a process of conjugation has recently been described, in which conjugation-tubes are developed either between pairs of cells or between the outgrowths from germinating spores. In one or two closely allied plants (e g *Zygosaccharomyces*, the Ginger Beer Yeast) it occurs just before spore-formation In this way a fusion of nuclei is effected. This has been very generally regarded as being of the nature of a sexual process, but it is doubtful if any sexual significance is to be attached to it; possibly it may correspond to the fusion of nuclei observed in young asci before free cell-formation begins (p. 550).

§ 29 **Alcoholic Fermentation.**—In the process of alcoholic fermentation induced by yeast, grape sugar is decomposed The chief decomposition products are alcohol (C_2H_6O) and carbon dioxide, but there are also minute quantities of glycerine and succinic acid The general equation might be represented thus —

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2$$

It has been shown that while the yeast cells thrive best in the presence of oxygen, *i e* while the growth and division of the yeast cells is most rapid in this condition, the weight of sugar transformed into alcohol and carbon dioxide *per unit weight of yeast* is much greater in the absence of oxygen and that, when oxygen is abundantly supplied, *relatively* little alcohol is produced

We have already had examples of similar decompositions in the digestion of stored food material effected by the action of definite chemical substances called unorganised ferments which can be extracted and act apart from living protoplasm Fermentation processes, such as that effected by yeast, differ in that the decomposition seems to depend essentially on the presence of living organisms The conclusion was arrived at that the protoplasm of such organisms could itself act as a ferment, and the organisms were spoken of as **organised ferments.** From yeast, however, a chemical substance, called *zymase*, has been extracted which can induce alcoholic fermentation, and recent work on enzymes on similar lines, tends to the conclusion that in all cases the action is due to the presence of unorganised ferments

§ 30 **The Meaning of Fermentation**—All plants must have a supply of energy for carrying on their metabolic processes and for the performance of internal and external work In most plants the necessary energy is liberated by oxidative decomposition to which the term of aerobic respiration is usually applied and most plants die if deprived of oxygen

Some plants, however, can obtain a supply of energy in another way which does not necessarily involve any con-

sumption of oxygen—namely, by breaking down the complex substances of which their food is composed, which process is usually termed anaerobic respiration (p. 184). In many cases it appears that the aid of ferments is invoked by the protoplasm in order to induce these decompositions, and it seems probable that this is true in all cases.

The term fermentation is a popular one, and is applied to cases of anaerobic respiration when the products of the latter are unusually conspicuous or abundant. The tendency to produce a ferment is so strong in the case of the yeast-plant that its production does not entirely cease even in the presence of oxygen, when the plant can obtain all the energy required by aerobic respiration.

Agaricus campestris—The Mushroom.

§ 31. **General.**—*Agaricus* is a very large genus including many subgenera and species. It belongs to the large group of Fungi called Basidiomycetes. Popularly most of the plants included in it are called "toadstools" and "mushrooms." Most of them are saprophytes, and are to be found in abundance in damp woods where the soil is rich in organic substance. A few, however, are parasitic, and very injurious to trees which they infest. Apart from this they all closely resemble each other in structure and in the general course of their life-history. *Agaricus campestris* is the common mushroom.

§ 32. **Habit and Structure of the Mushroom** (Fig 328) —The mushroom is a saprophyte. It lives on decomposing organic substances (humus) in meadows and other localities The part of the fungus which is seen above ground—the part which is called the toadstool or mushroom—is only the reproductive structure, the fructification or **conidiophore.** This is developed on a delicate filamentous **mycelium,** the vegetative body or thallus, which ramifies through the soil and absorbs the organic compounds on which the fungus lives.

The so-called "mushroom-spawn" so largely used in the cultivation of mushrooms, consists simply of compacted

blocks of well-manured soil containing a tangled mass of mycelial hyphæ. If these be buried in a suitable locality (*i.e.* damp and rich in humus products), the mycelium grows and develops conidiophores

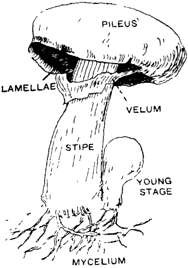


Fig. 328.—The Mushroom.

The much-branched filamentous **mycelium** is incompletely septate, *i e* the segments into which the septa divide the hyphæ are cœnocytic The hyphæ are colourless, and contain vacuolated protoplasm with nuclei and oil-globules Frequently the hyphæ may be found running in strands, and anastomoses between them are not uncommon.

§ 33. **Reproduction.**—The reproduction of *Agaricus* is asexual, being effected solely by means of **conidia.** Sexual reproduction has not yet been discovered in *Agaricus.*

§ 34 **The Conidiophore** (Fig. 328), on which the conidia are produced, is a very massive organ It seems altogether different in its structural characters from the filamentous mycelium on which it is developed. Examination shows, however, that it is really a false tissue (p 537), consisting of compacted interwoven hyphæ resembling those of the mycelium. It consists of a massive circular umbrella-shaped head, called the **pileus,** borne on top of a stalk, the **stipe.**

The upper surface of the pileus is more or less rounded

and convex. In the different species of *Agaricus* it shows an immense variety of colour, due to the presence of colouring matters in the cell-walls The under surface bears a large number of delicate vertical plates radiating from the stipe to the edge of the pileus These bear an external resemblance to the gills of fishes, and are spoken of as the **gills** or **lamellæ**. In the Mushroom they are flesh-coloured when young, but become a rich chocolate brown when fully developed, and covered by innumerable brown or black conidia

Encircling the stipe, close to the attachment of the pileus, are the remains of a membrane which originally extended from the stipe to the edge of the pileus and closed in the "gill-chamber." This torn membrane is called the **velum.**

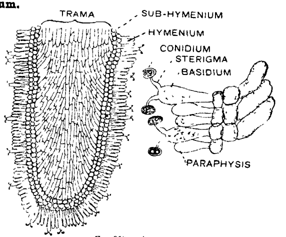


Fig 329. —AGARICUS.

Section across one of the gills The diagram to the right represents the hymenium and sub hymenium more highly magnified
(Four conidia should have been shown on each basidium.)

§ 35 **Structure of the Conidiophore.**—The hyphæ in the cortical region of the stipe are densely compacted, but the central or medullary region consists of loosely interwoven hyphæ with numerous spaces between them

If a vertical section be taken across a lamella it shows the following structure (Fig. 329). There is a central core of interwoven hyphæ known as the **trama.** These hyphæ curve outwards towards the surface of the lamella, and end in small cells, which form what is known as the **subhymenial layer.** Outside these again, forming the superficial layer of the lamella, are larger, rather stout and slightly elongated cells This is the **hymenium** or *hymenial layer*

The cells of the hymenium are of two kinds: (*a*) barren cells called **paraphyses;** (*b*) cells called **basidia.** Each basidium bears at its apex usually four slender processes called **sterigmata,** and from each sterigma a small rounded conidium or basidio-spore is abstricted.

Each basidium has at first two nuclei. These fuse together By division of the resulting nucleus four nuclei are formed, one of which passes into each conidium or basidiospore.

§ 36 **The conidia** are produced in great abundance This can be demonstrated by laying a ripe pileus for some time on a sheet of paper. A sort of print of the under surface of the pileus is obtained owing to the thick deposit of conidia The conidia when ripe fall off, and, if they reach a suitable soil, they germinate Each sends out a hypha, which grows and branches and produces a new mycelium. The germination has only been observed after considerable difficulty. The growth of the mycelium from the conidium is slow, and conidiophores are not produced till after a lapse of seven or eight months

§ 37. **Development of the Conidiophore.**—Fig. 330 shows various stages in the development of the fructification. It makes its appearance on a strand of the mycelium as a tiny rounded or pear-shaped body, consisting of a tangle of hyphæ At first there is no distinction between stipe and pileus, but, as growth goes on, the apex of the developing structure expands to form the pileus. In this, towards its lower surface and completely enclosed in the tissue, an annular cavity appears. In the roof of this

cavity the lamellæ are differentiated, and its floor becomes thin and membranous, forming the velum, which is ruptured towards the close of development.

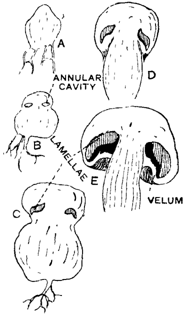


Fig 330 —AGARICUS
Stages in development of conidiophore. (Diagrammatic longitudinal sections)

BACTERIA (= SCHIZOMYCETES).

§ 38 **General.**—The Schizomycetes, commonly spoken of as Bacteria or Fission-fungi, form a group of extremely minute organisms, destitute of chlorophyll, which play a part in organic nature altogether out of proportion to their size By some they are placed among the Fungi; others place them with the *Cyanophyceæ* (see p. 511) in a special

division called the *Schizophyta*. Probably they are best regarded as a distinct group of Thallophyta. The organisms may be unicellular or multicellular. The multicellular forms may be filamentous, or form cell-plates or cell-masses; they are to be regarded, however, as essentially aggregations of unicellular forms. Bacteria are ubiquitous organisms, being found in the most unexpected media —river water, sulphur springs, etc.

The mode of life is parasitic or saprophytic. Many forms parasitic on animals are harmless, sometimes even beneficial, others (pathogenic forms) prejudicially affect the normal physiological processes and produce pathological or diseased conditions. Most of our infectious diseases have been shown to be due to the ravages of bacteria, which are popularly called "*germs*" or "*microbes*." They are present in the air or in various media, and in favourable circumstances reproduce themselves with great rapidity A single germ may give rise to millions in the course of a day or two. This explains why many of these diseases are infectious and become epidemic.

The saprophytic forms thrive in various organic media and produce characteristic fermentative changes. Well-known examples are the souring of milk and the conversion of alcohol into acetic acid in the formation of vinegar. Bacteria, however, never induce alcoholic fermentation. The disastrous effects of infectious diseases are also in many cases due to the formation of poisonous waste products (toxins) which accumulate in the blood

In all these processes bacteria seem to act as organised ferments From some bacteria, however, unorganised ferments have been extracted, which are capable by themselves (*i e.* apart from the living cells) of producing the characteristic fermentation (see p. 559). Most bacteria can live only in the presence of oxygen, and are said to be **aerobic**, but many cannot live in the presence of oxygen, and are called **anaerobic.** Others again can live both in the presence and in the absence of oxygen. The significance of this capacity for doing without oxygen, and its relation to the process of fermentation, have been sufficiently dealt with in connection with the yeast-plant.

Putrefaction is a process of fermentation set up by certain species of bacteria in proteid substances, and is usually accompanied by the evolution of offensive gases In this way these complex nitrogenous substances are gradually decomposed into ammonia and other compounds In the soil by the action of bacteria the ammonia is acted on, and first nitrous and then nitric acid produced. This is the process of **nitrification** (p 164) In this way dead organic substance is first decomposed and then brought back into forms available for absorption by green plants These are essentially processes of oxidation The bacteria act as carriers of oxygen in virtue apparently of the production of ferments known as *oxidases* which act by oxidising not by hydrating as in the case of most ferments

It is interesting to notice that a few Bacteria including the nitrifying organisms by a process of fermentation obtain a supply of energy which enables them to build up organic materials from carbon dioxide and water in the absence of chlorophyll and without the aid of light We have also indicated (p 164) that there are Bacteria in the soil which can bring free nitrogen into combined form It is probable that the bacteroids present in the root tubercles of leguminous plants are bacteria of this kind they have been called *Bacillus radicicola*

§ 39 **The Bacterium cell** —The cells are extremely microscopic a diameter of less than $\frac{1}{20000}$ of an inch being quite common They can be examined only under very high powers of the microscope, and even then the structural details cannot be made out with certainty

Each cell has a distinct cell wall In many cases this apparently does not consist of cellulose but of a chitinous substance The cells contain granular protoplasm in which vacuoles may occur Nuclear substance in the form of chromatin granules occurs in many but the presence of a definite organised nucleus has not been demonstrated There are no plastids, but in one or two chlorophyll is found, and in others various pigments occur. In a few forms a granular substance has been observed, giving a

blue or purple reaction with iodine, being probably therefore some kind of starch.

There are many different forms of cells (Fig. 331). Very minute spherical forms are called **cocci**, or *micrococci*; elongated rod-like forms, **bacilli**; spirally coiled forms, **spirilla**; comma-like forms, **commas**. These are the commonest. Sometimes filaments of bacteria are aggregated in enormous numbers and held together by mucilage, forming a sort of scum on decomposing liquids. This is known as the **zooglœa** condition (Fig. 332, A). Sometimes the cells form cell-masses.



FIG 331 —FORMS OF BACTERIUM CELLS A, Micrococci, B, Bacilli, C, Commas, D, Spirillum with flagella

These different forms are not necessarily to be considered as characteristic of different species. The same species may pass through a number of forms at different stages. They are to be regarded rather as "**growth forms**," *i.e.* forms assumed at different periods of growth. In other words, the bacteria are *polymorphic*, although probably not to the extent hitherto believed.

Many bacteria have the power of independent movement. This is in many cases effected by means of very slender cilia or **flagella**, which are apparently outgrowths, not of the protoplasm, but of the cell-wall. A cell may have one, two, or a number of these.

§ 40 **Reproduction.**—There are two methods of reproduction. Both are asexual. In the process known as "**fission**," the parent-cell undergoes division into two daughter-cells. It is simply a process of cell-division in a unicellular organism. A micrococcus cell simply becomes constricted and divides into two; a bacillus divides transversely.

The other method of reproduction is that of "**spore**"-**formation** (Fig. 332, B). It is commonly seen in bacilli, and as a rule it takes place in the zooglœa stage. The protoplasmic contents of the cells, starting from a small centre, gradually round themselves off, and aggregate in

the middle of the cells. A new cell-wall is then formed round the protoplasmic mass When fully formed, this cell-wall is extremely firm and resistant Thus the "spores" are produced inside the cells, usually one in each cell, but sometimes more than one (endosporous formation) The spores can withstand great extremes of heat and cold without injury They may remain quiescent for a considerable time if the conditions are unfavourable, but are eventually set free by the decay of the walls of the parent cells When a spore germinates, the outer membrane is ruptured, and the contents escape as an ordinary bacterium-cell.

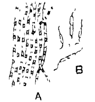


Fig 392.—SPECIES OF *Bacillus*
A, Zooglœa stage with spore-formation, B Motile stage

§ 41. **Bacillus subtilis** will serve as an example It is the hay-bacillus If hay be chopped up and either soaked or boiled in water and kept for some little time, numerous bacillus cells can be recognised if the fluid be examined under a high power Each cell is a tiny rod-shaped body having the structure above described. It bears a number of flagella. In this stage the cells multiply by fission, but after a time they pass to the surface and form a scum (zooglœa stage). If this be examined the cells will be found aggregated into long filaments embedded in a mucilaginous substance, formed by the disorganisation of the outer layers of the cell-walls It is in this stage that the spores are developed. They are extremely resistant, and can withstand boiling for a considerable time They germinate in the usual way in a suitable medium

SUPPLEMENT.

EVOLUTION AND GENETICS.

§ 1. **Genetics** is the modern scientific study of Variation and Heredity It has been described as the practical study of the Physiology of Heredity and Variation, and proceeds mainly by the method of experiments in the culture and breeding of plants and animals Of recent years it has become more and more closely associated with Cytology, which has lent valuable aid by correlating the finer structure of the germ-cells with some of the observed phenomena Besides considering some of these practical studies, and the bearing of the results obtained on the Theory of Organic Evolution, we shall also give some account of **Biometry,** that is, the statistical and mathematical study of Variation and Heredity associated with the names of Galton, Weldon, and Pearson.

§ 2 **Heredity** has been defined as the process or method by which the constitution and characteristics of organisms are transmitted to their offspring; or, in a more general way, as the genetic relation between successive generations of organisms, in virtue of which offspring *tend* to be more or less like their parents. The resemblance, however, is never complete; there are differences A Theory of Heredity, *i.e.* a theory which aims at explaining the working or mechanism of heredity, must account for the differences as well as for the resemblances.

§ 3. **Germ-Cells and Germ-Plasm.**—In sexual reproduction two germ-cells, male and female, fuse to form a zygote from which a new individual is produced by a

process of development, of the mechanism and dynamics of which, apart from theory, we are almost completely ignorant. It is evident that the transmission of characters must in some way be effected by the germ-cells. Many suggestive facts have led to the conclusion that the bearers of the hereditary characters are located in the nuclei of the germ-cells and more especially in the chromosomes. The hypothetical substance concerned in the transmission constitutes the germ-plasm, "a specific substance of definite chemical and molecular structure which is the bearer of the hereditary qualities." A few biologists, however, believe that the cytoplasm of germ-cells may also play a part, more especially in the transmission of the more plastic characters.

Most biologists now believe that the germ-plasm consists of representative particles or primary constituents by which the characters of the adult organism are largely determined; and Mendelians more especially hold that the characteristics of organisms can be analysed into definite unit characters represented by particles to which the names *germinal factors, genes, determiners* have been given. There has been much discussion as to the nature of these factors. Some hold that they are protoplasmic, while others have suggested that they may be more of the nature of substances capable of producing enzymes or ferments. There is also experimental evidence that each germ-cell has a full set of factors representative of the characters of an adult organism, so that the germ-plasm of the zygote would hold a double set. In this connection it should be remembered that the number of chromosomes in the nucleus is doubled at fertilisation.

§ 4 **Continuity of the Germ-Plasm.**—This theory, first definitely enunciated by Weismann, emphasises the special and, indeed, unique character of the germ-plasm as a substance handed down directly from generation to generation, for the most part independent of and isolated from the somatic or body-cells of the individuals in whose germ-cells it is found. The idea is that in the developing zygote the cells which will eventually produce germ-cells are kept distinct from those which go to form the various tissues and organs of the adult body. In other words, the germ-cells are not derived from body cells, but from cells which have

never been differentiated and whose special function it is to produce them. It is essentially a theory of heredity and explains in a general way why offspring tend to resemble their parents The germinal factors are handed down from generation to generation and, provided there is similar development, we should expect resemblance not difference in the adult characters. Differences in heritable characters (variations) are due to the fact that the germ-plasm may undergo modification during transmission.

While this theory is now definitely accepted by biologists the degree of isolation and seclusion of the germ-cells from external influence postulated by Weismann cannot be maintained, especially in plants. It is important also to bear in mind that as the germ-plasm increases in amount and undergoes subdivision it must necessarily be nourished, and therefore be subjected to metabolic influences.

§ 5 **The Inheritance and its Expression.**—While the general term *Inheritance* has been, and may be, taken as synonymous with the term *Heredity*, it is well to distinguish clearly between this and *the inheritance* or *what is inherited* It is customary to speak of certain characters of the adult organism as *inherited*, but, strictly speaking, what is really passed on to the offspring is the organised zygote, the most important part of which is the germ-plasm or the complex of germinal factors with all its potentialities The adult organism, with the sum-total of its characters, represents the development or expression of the inheritance

The inheritance requires for its development a suitable environment, and hence the characters which actually appear in the adult organism will depend not only on the constitution of the germ-plasm of the zygote, but largely also on the environment in which the organism develops Those characters, however, which appear to be determined essentially by factors present in the germ-plasm, and which in a normal environment regularly reappear in the offspring, are said to be inherited, they are the heritable or inborn characters of the organism

On the other hand, the power of making responses (often very definite and purposive) to environmental influence is a part of the organism's inheritance Characters induced in this way are called modifications, formerly they were called "acquired characters." They are characters acquired during

an individual's life as the result of environmental influence They will reappear in the offspring under the same conditions of environment, but are not for this reason said to be inherited, but simply to be reacquired. Under changed conditions they do not reappear As examples may be mentioned the different characters developed by plants according as they are grown in dry or in moist conditions, on land or in water, in sun or in shade, on high hills or in the low ground. In recent years the extent to which organisms can be modified by external influences has been demonstrated by many remarkable experiments.

§ 6. **Inheritance of "Acquired Characters."**—By this is meant, not the reappearance in the offspring of the same modificational characters under the same conditions of environment, but that a modification induced in the body of the parent can *in some way* influence the germ-plasm of the germ-cells and effect a change or alteration of the germinal factors of so definite and representative a kind that the same character or structure appears in the offspring *even in the absence of the particular environmental conditions* which induced it in the parent, so that its reappearance is no longer dependent on environmental influence, but on germinal factors which form part of the inherited equipment It is known as the Lamarckian Factor or Principle in Evolution.

Many biologists, more especially in France and America, regard it as an important factor, although they do not accept the principle in its original crude form (enunciated by Lamarck in 1809), they believe that the modifications, affecting the metabolism of the organism, may by repeated impress in successive generations bring about, possibly by the action of ferments or other substances, first an alteration of a definite kind in the cytoplasm of the germ-cells, and ultimately a representative change in the germ-plasm located in the nuclei. There is, however, no generally accepted evidence in favour of it, and, indeed, it is very difficult to conceive or picture any mechanism whereby representative changes of such a kind could be produced in the germ-cells. Many biologists, therefore, repudiate it

altogether, while others, who would otherwise be ready to welcome it as an additional factor in evolution, prefer to suspend judgment and regard the matter as unproved.

This question, however, must not be confused with the question as to the possibility of environmental influences directly or indirectly affecting the germ-cells and producing germinal changes, not representative of any somatic modification, which lead to variation. There is some evidence that germinal variations may be caused in this way

§ 7. **Variation.**—Differences in character between offspring and their parents, or between the individuals of a family or species, which are due to changes or modifications in the germ-plasm, are called Variations. There are many different kinds of variation, but they may be included under two main forms known as *Continuous* and *Discontinuous* These were clearly distinguished towards the close of last century by certain biologists (Bateson, Hugo de Vries, and others) who had become impressed by the importance of Discontinuous Variations and the necessity for the more scientific study of variation and heredity

Continuous Variations with regard to any character are those deviations from the specific or racial mean affecting all the members of a species or race in different degree, so that, as exhibited in a large number of individuals, they can be arranged in a continuous series with imperceptible gradations between two extreme values. The meaning of this will become clear in what follows It was on small individual variations of this kind that Darwin mainly relied in his Theory of Evolution (see Chap XVIII).

Discontinuous Variations are more or less sharply marked, abrupt, or sudden deviations from the type of the species or race, with regard to one or more characters, which are exhibited by one or more individuals, but are not connected by intermediate steps with the mean or type of the species These are the variations to the very marked or extreme forms of which the names "sports," "breaks," "monstrosities," have been applied They may all be included under the general term **mutations.** The individual showing the mutation is now called a *mutant*,

and the germinal change which determines the mutation is called a *premutation*

Examples of mutation in plants are found in the sudden appearance of forms with cut or laciniated leaves or petals, of double flowers, of differently coloured flowers, of dwarf forms, of weeping varieties of trees, of red-leaved forms, or hairless varieties. It is believed also that many at least of our varieties of cultivated plants have arisen in this way

The recognition of the importance and frequent occurrence of discontinuous variations was chiefly due to Bateson Hugo de Vries of Amsterdam carried out a large amount of work on the experimental side He cultivated thousands of seedlings of different plants in the hope of recognising such variations He succeeded in finding a plant, Oenothera Lamarckiana, which was producing numerous mutations and some at least of the mutants bred true He had, in fact, found a plant which seemed to be throwing off new species by mutation.

There was thus a presumption that the characters which distinguish natural species had originated in the same way, and the impression that mutations were variations of the utmost importance in evolution gained ground This view was strengthened by the discovery of Mendel's work in 1900 (see § 17), for the Mendelian unit characters appeared to be of the same nature as the characters distinguishing species and they were shown to be subject to perfectly definite laws of inheritance

§ 8 **The Mutation Theory.**—The doctrine of the origin of new species by mutation was definitely enunciated in the Mutation Theory of de Vries (1901-3) According to this theory mutations are the variations of real importance in evolution; new species arise, not by the continuous action of natural selection on small individual variations, but at one step by abrupt or sharply marked mutations

§ 9 **Modes of Inheritance.**—It has been customary to recognise different ways in which characters may be inherited. In (1) *Blended Inheritance* the offspring, with regard to one or more

characters, is intermediate between the two parents, the parental characters are blended in the offspring. The blend may be an intimate one, or the character of one parent may be more or less prepotent, so that there is stronger resemblance to that parent There is (2) *Exclusive Inheritance* when the character of one parent is absolutely prepotent and the offspring therefore resembles that parent only with regard to the character considered. In (3) *Particulate Inheritance* the offspring shows the paternal character in one part and the maternal in another Instead of a blend there is, as it were, a coarse mixture For example, while one parent may be hairy and the other glabrous, the offspring may be hairy in one part and glabrous in another. In (4) *Alternative Inheritance* some of the offspring show the paternal character and others the maternal In this case the paternal and maternal characters appear to depend on germinal factors inherited as distinct units, there is no blending (5) *Reversion*, when the offspring show a character possessed not by the parents, but by some more or less remote ancestor

Although many biologists have maintained that Mendelian principles could only apply to Alternative Inheritance and certain cases of Exclusive Inheritance, it now seems probable that they are capable of explaining all these different forms or modes of inheritance

§ 10 **Biometrical Study of Variation**—This has been applied to continuous variation in respect of such characters as lend themselves to measurement or to counting In the simplest cases the method consists in the measurement or counting of a character in a large number of individuals All the measurements or counts (called *variates*) are arranged in groups or *classes*, the measurement or count in each class being the same, and the number of individual measurements or counts in each class (*i e* the number of variates in each class) is called the *frequency* of that particular measurement or count A graph may be drawn in the usual way showing the relation between the measurements or counts and the frequencies.

EXAMPLE—The length of the lowest fruit in 568 plants of Oenothera biennis was measured. The results were:—

Length of Fruit in mm	15,	16,	17,	18,	19,	20,	21,	22,	23,	24,
Frequency . ..	1,	1,	5,	11,	17,	27,	37,	62,	74,	83,
Length of Fruit in mm	25,	26,	27,	28,	29,	30,	31,	32,	33,	34
Frequency	79,	51,	43,	32,	18,	13,	5,	5,	3,	1.

Here there are 568 variates arranged in 20 classes. In the graph (Fig. 333) the longest ordinate (the mode) indicates the measurement of greatest frequency—that is, in this case, the length of fruit most frequently found (approx. 24·2 mm.). This is known as the modal value The frequency gets less and less the greater the deviation (+ or −) from the modal value

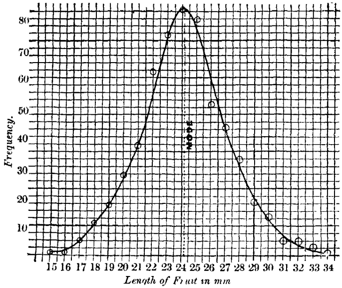


Fig 333

The points indicate the actual frequencies obtained, the curve as drawn amongst the points may be taken to represent approximately the normal curve of variability

The more numerous the variates and the classes in which they are grouped (depending on the unit of measurement employed), the more definite does the curve appear and the more nearly, as a rule, does it approximate to an ideal curve called the *normal curve of variability* (Fig. 333).

In this case the modal value would coincide with the mean or average of all the measurements. When the variation is of this type it is called *normal variation*. In our example the mean or average is nearly 24·2 mm., and this agrees closely with the modal value

The form of the curve will indicate the nature of the variation. If there is a wide range of variation the curve will tend to be wide, if there is a narrow range, the curve (with equivalent scale of representation) will be narrow and steep. It is possible also, in each case, to calculate a quantity or number (represented by σ) called the *standard deviation* which will indicate or represent the variability or amount of variation with regard to the character considered. It is calculated as follows.—Square the deviation (whether + or −) of each class from the mean or modal value; multiply each square by the corresponding frequency, add products; divide sum by total number of variates, take the square root, (multiply by the number of units in the class range if it is not unity). For our example the standard deviation is 3·2.

It is also possible to determine a quantity or number, called the *coefficient of variation*, which enables a comparison to be made of the variability of different characters in the same plant or in different plants, although different units of measurement may have to be employed. The coefficient of variation is simply the standard deviation expressed as a percentage of the mean or modal value. In our example it is 13·2.

The same kind of curve is obtained if, say, 8 pennies are tossed up 256 times, the tosses arranged in classes according to the number of heads (or the various combinations of heads and tails) which turn up, the frequencies noted, and the results plotted. The *probable* frequencies of the various combinations can be arrived at mathematically by expanding $(1 + 1)^8$. They are 1, 8, 28, 56, 70, 56, 28, 8, 1, i.e. 8 heads (0 tails) once, 7 heads (1 tail) 8 times, 6 heads (2 tails) 28 times, and so on. Actual experiments agree pretty closely with these probable results. Data for other cases can be calculated by expanding $(1 + 1)^n$, giving n different values. n will represent the number of coins and 2^n will be the number of throws. The ideal curve to which such curves approximate is the *Curve of Probability* or the *Normal Curve of Frequency*.

Such curves, obtained experimentally, are simply the expression of probable results or happenings depending on

such a large number of small independent causes that we usually say they are due to chance—they follow the laws of chance. Usually the causes will act equally in the two directions, and hence the frequency will be greatest for equal numbers of heads and tails, the extreme results (all heads or all tails) are due to all the causes happening to act in one direction only. So with normal variability The question, however, arises as to whether the causes to which it is due are germinal in nature or environmental Darwinians would say that they are, largely at any rate, germinal; mutationists, on the other hand, maintain that they are mainly environmental (see § 15)

The variability curve obtained may not be quite symmetrical about the modal ordinate In this case it is said to be *skew*, and the modal value will depart more or less widely from the mean or average of the measurements The amount of skewness varies In extreme cases the curve may be all on one side of the longest ordinate. As an example plot the curve expressing the variation in the number of petals in the Buttercup

Number of petals	5,	6,	7,	8,	9,	10,	11
Frequency	133,	55,	23,	7,	2,	2,	0

It has been shown that these asymmetrical or skew curves also in many cases correspond or can be fitted to theoretical mathematical curves

Biometricians maintain that by statistical study, repeated at intervals on different generations, of the variability in a population (*i.e.* any assemblage of organisms of the same species in a particular area) it is possible to determine, by observation of the differences that have occurred, whether natural selection has been acting and, if so, in what particular direction In this connection it should be noted that occasionally graphs with two (or more) humps, more or less distinct, i e with two (or more) frequency maxima, are obtained Darwinians would say that here we have evidence of the separation of the species, owing to natural selection, into two (or more) varieties or species On the other hand, mutationists would hold simply that there has been sharply marked discontinuous variation or mutation with continuous variation about each type

In our example a single measurement of a character was made on each individual In studying variation in a population or species, however, a number of measurements in each individual may be made For example, in studying the variation in the number of lateral veins in Beech leaves, the number of veins might be counted in, say, 20 leaves from each of 100 Beech trees. On the other hand,

the variation in the development of a character in a single individual may be studied, as, for example, when the lateral veins in a large number of leaves from the *same* Beech tree are counted, or separate weighings are made of a large number of seeds from the same plant In this case it would be found that there was a modal or mean value for the individual different from that for the population or species Each individual would show a distinct type.

§ 11 **Biometric Study of Heredity.**—Similar statistical and mathematical methods as for continuous variation have been employed. In the simplest case they are applied to blended inheritance and to characters which show normal variation in parents and offspring It will be sufficient to describe briefly the two main results arrived at They are the Law of Filial Regression and the Law of Ancestral Heredity (or Law of Ancestral Inheritance).

§ 12 **Law of Filial Regression.**—Suppose that in a population the modal value of a certain character which shows normal variation is M and that a large number of individuals in which the development of the character is represented by $M + h$ (the deviation from the modal value being $+ h$) are selected as parents, and the variation of the same character in the offspring is studied in the usual way, then it is found that the modal value of the character in the offspring is intermediate between M and $M + h$, in other words, there has been partial regression to the mean or mode of the general population Similarly, where the deviation of the parents is $- h$ the modal value of the character in the offspring lies between $M - h$ and M, again, there is partial regression to the mean or mode of the general population This would be found to hold good generally from whatever class of variants the parents were selected.

The Law of Filial Regression is simply that the deviation of offspring from the specific type or from the mean of the general population is *on the average* less than that of their parents It is the law which expresses the tendency of offspring to keep up the specific average. The explanation which is given of this by biometricians is that

the inherited characters of offspring are derived not merely from parents but from a long line of ancestors, and "the mean of that ancestry is probably not far from that of the general population" This explanation will be considered later (§§ 13, 15).

§ 13. **Law of Ancestral Heredity.**—There is regression because the inheritance of parental characters is not complete If there were complete regression the inheritance from parents would be nil, if the modal value of the character in the offspring were equal to the value of the character in the parents there would be complete inheritance which would be represented by unity The ratio between the modal deviation of the offspring from the mean of the general population and the deviation of the parents from the general mean, might be taken to represent the degree of hereditary resemblance between offspring and parents The offspring of all classes of variants might be considered in the same way

Now, when this is done, it has been found possible to arrive at a general ratio which will represent the *average* degree of hereditary resemblance between parents and offspring for any particular character, and this, *it is maintained*, may be taken to represent the intensity of inheritance, or the *amount of the inheritance* derived from the parents This ratio is called the *Coefficient of Heredity*, or the *Coefficient of Correlation* between offspring and parents Similarly, without specifying certain refinements in method, it is possible to arrive at ratios which will represent the amount of hereditary resemblance to, and hence (so it is said) the amount of the inheritance derived from, the various ancestors.

By such methods Galton arrived at his "Law of Ancestral Heredity" According to this law the *average* contributions to the inheritance or to the heritable characters of an individual by the two parents, the four grandparents, the eight great-grandparents, etc, can be represented by definite fractions forming a geometric series, namely, ·5, ·25, ·125, etc, the sum of the series being, of course, unity, representing the whole inheritance. Pearson modified

Galton's fractions and gave a more rapidly diminishing series ·624, ·199, ·063, etc

The law is to be regarded as a general statement of what happens *on the average* when inheritance in a population is considered As Pearson has said the Law of Ancestral Heredity "predicts the *probable* character of the individual produced by a given ancestry"; or, again, "Of the individual we can assert nothing as certain, only state the probable; . . . all we know in heredity [from the biometric point of view] is what degree of resemblance there is on the average" Mendelian experiment also clearly shows that this is the only possible way of interpreting the law by proving that in certain cases an ancestor may contribute nothing to the inheritance

We shall refer to the law again (§§ 15, 21), but meanwhile it may be remarked that the average degree of resemblance between individuals and their various ancestors, as measured by the Coefficients of Correlation, is taken as a measure of the amount contributed by the various ancestors to the inheritance It is open to question whether this interpretation is valid and whether the idea of inheritance involved in all this is the same as is expressed in § 5 Further, according to Mendelian theory each germ-cell contains only *one* complete set of factors representative of the characters of an adult organism and the zygote therefore a double set On this view it is difficult to see exactly what is meant by contributions to the inheritance from the various ancestors.

§ 14 **Effect of Selection.**—Assuming the truth of the Law of Ancestral Heredity for blended inheritance and for characters showing normal variability, Pearson calculated in a particular case that, if individuals, showing with regard to the character studied a deviation h from the mean of the population, be selected as parents *in successive generations*, the result of selection would be the development in the offspring on the average of ·62h in the first generation, ·82h in the second, ·89h in the third, and, after a few generations, over ·90h, i e. after a number of generations selection will result in the development of the character to over 90 per cent. of the value selected · but further selection will have little or no effect, and if, at any stage, selection be stopped and the stock inbred, then the offspring will regress to the general mean of the original population.

§ 15 **Johannsen's Pure Line Theory (1903).**— Johannsen, Professor of Botany at Copenhagen, experimented with Kidney Beans and other plants, and arrived at conclusions which have an important bearing on questions of variation and heredity He defined a *pure line* as consisting of all the descendants of a single individual by continued self-fertilisation This means that the offspring in each generation have one parent only, and there is no mixing of different germ-plasms from two parents

He took a number of seeds from 19 Bean plants. With regard to seed weight they showed normal variability, and he determined the mean or average seed weight of the population. He sowed the different lots *separately* and thus separated the population into 19 pure lines He found in each pure line that, while there was nearly normal variability of wide range, there was a *distinctive* mean weight of seed

Further, on arranging seeds *of any one of the pure lines* in classes according to weight, sowing these separately, and determining the mean weight of seeds produced by each set of offspring, he found *in all cases* that it approximated to the mean seed weight of the pure line from which the classes of seeds were taken. This means that the variation in seed weight within each pure line had not been inherited, within a pure line selection has no effect The explanation of this would seem to be that the normal variations in a pure line are really not variations at all in the sense of being due to germinal changes, but are of the nature of modifications due to environmental influences The same explanation would be given of the normal "variation" in the development of a single character in *one* individual, *e g.* seed weight, number of lateral veins in the leaves, etc It is to "variations" of this kind that the term "fluctuations" is more strictly applied

Johannsen found, however, that *in a population*, which may be regarded as consisting of a large number of pure lines of different type, selection was effective up to a certain point This agrees with Pearson's calculation (p 580) The explanation here would seem to be that selection results in the separation of the pure line which, with

respect to the character selected, shows greatest deviation from the mean of the population It is believed that the pure lines of different type in a population or species have originated as small mutations, and, after the limit is reached, selection will only be effective provided there is further mutation There is some evidence that these small mutations in their inheritance on crossing follow the law of Mendel

It would seem, therefore, that the continuous variation shown by a population or species is made up of two distinct parts—small mutations on the one hand, and, on the other, about each mutation, fluctuations of the nature of environmental modification, the fluctuations about all the mutations overlapping and thus producing a continuous normal curve. This conception of continuous variation in a population, in which the pure lines are constantly being intermixed by crossing, would seem to be adequate to account for the facts of regression and inheritance in such a population without having recourse to the conception of ancestral contributions to the inheritance

§ 16 **Hybridisation.**—Experiments in hybridisation, more especially with forms not too widely different from each other, would seem to offer the best hope of solving the problems of heredity and variation The term *hybrid* is now commonly applied to the offspring of two individuals which differ more or less distinctly from each other in one or more characters. This indeed was its original significance, although afterwards it came to be restricted to the offspring produced by the crossing of individuals of distinct species Cases are now known of hybrids produced by crossing distinct genera.

In the process of hybridisation in Flowering Plants the young undeveloped anthers are removed by means of forceps from one or more flowers of one plant A, and the stigmas, when they are mature, are touched by an anther transferred to them, by means of forceps, from the other plant B The flowers to be pollinated must, of course, be protected from access of other pollen, *e g.* by parchment bags, and other precautions must be taken With a few

exceptions apparently, it makes no difference whether A pollinates B or B pollinates A. The hybrid embryos are in the seeds produced in the ovaries of the flowers artificially pollinated.

The results obtained by the many hybridists before Darwin's *Origin of Species* appeared were very conflicting, and contributed little of any value to the elucidation of the problems of heredity and variation The hybrids might be more or less distinctly intermediate in character between the parents, or they might resemble one parent in some characters, and the other parent in others, and so on. The offspring of hybrid plants in succeeding generations often showed an extraordinary variety of forms, and hence it was usually believed that hybridisation gave rise to great variability. In many cases it was found that the hybrids showed a distinct increase in vigour as compared with the parental forms, the explanation of this has not yet been satisfactorily found Finally, hybrids produced by crossing distinct species were usually more or less sterile Mendel found the true method of experiment, but his work was lost sight of for 35 years.

§ 17 **Mendel and His Work.**—Gregor Johann Mendel (1822-1884) was a monk in the Monastery of Brunn in Bohemia, he became Abbot in 1868 His most important experiments were made in the garden of the monastery from 1857 to 1865 The results were communicated to the Natural History Society of Brunn in 1865, and published in the *Proceedings* in 1866 In 1900 they were rediscovered independently by three botanists—Hugo de Vries, Tschermak, and Correns—and in the search to find if anything of the kind had been done before, Mendel's paper came to light.

Mendel's methods and experiments provided the sure foundation for genetic research. He used certain varieties of Pea, mostly of the Edible Pea (***Pisum sativum***). His success was largely due to his attending to the following points —(*a*) he was careful to work with pure homogeneous material—the varieties of Pea were pure or bred true; (*b*) he considered each character separately, (*c*) he

recorded the offspring of each individual separately; (*d*) he kept records up to at least the third generation. The advantages of using varieties of Pea for experiment were that they showed constant, readily recognisable differentiating characters, the flowers were regularly self-pollinated and the hybrids perfectly fertile

Mendel fixed on a number of pairs of differentiating characters by which his varieties of Pea were distinguished —yellow or green cotyledons, smooth or wrinkled seeds, tall or dwarf habit (long or short stems), etc He considered each pair separately.

He crossed a pure tall variety with a pure dwarf variety, and found that *all the hybrid offspring*, constituting what is now called the first filial generation, F_1, *were tall*, and thus resembled the tall parent The tall character, or character of tallness, therefore, he called the *dominant character* He allowed these tall hybrid plants to fertilise themselves, and kept careful record of all the offspring, constituting what is now called the second filial generation, F_2 He found they consisted of talls and dwarfs in the ratio 3 · 1 (actual numbers obtained were 787 · 277)

The character of dwarfness, therefore, had simply been latent or unexpressed in the first or hybrid generation, Mendel called it the *recessive character*. He found that if these dwarf plants, forming one-quarter of the second generation, were allowed to fertilise themselves they produced nothing but dwarfs, *i e* they bred true and were pure for the dwarf character (*pure recessives*). When, however, the tall plants of the second generation were allowed to fertilise themselves, he found that while one-third of them (constituting one-quarter of the whole second generation) produced tall offspring only and were *pure dominants*, the remaining two-thirds (constituting one-half of the whole second generation) were *impure dominants* or hybrids, resembling the hybrid plants of the first generation, and, like them, producing tall and dwarf offspring in the ratio 3 1. Thus, in the second generation F_2, *pure dominants*, *hybrids* (or impure dominants), and *pure recessives* are found in the ratio 1 2 1

This can be graphically represented as in Fig 334

The crossing of the two forms is represented by D × R; the successive filial generations by F_1, F_2, etc., the dominant character by D, and the recessive by R, a pure dominant by DD, a pure recessive by RR, and an impure dominant or hybrid by D(R).

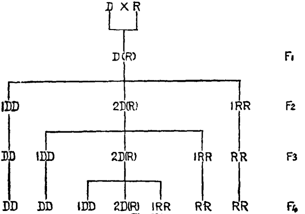


Fig 334

The most remarkable feature is the segregation or separating out, in definite ratio, of pure types from hybrid in the second and succeeding generations. The explanation of this was also given by Mendel. It was that the germ-cells (pollen grains and egg-cells, according to Mendel) produced by the hybrids were separated off or segregated into two equal groups, half of the male and female cells bearing the dominant character (or, rather, as we would now say, the dominant factor), and the other half bearing the recessive factor.

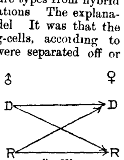


Fig 335

It is evident that in self-fertilisation the chances of a dominant or a recessive ♂ cell meeting with a dominant or recessive ♀ cell are equal, and the possible combinations in the zygote are thus, as indicated by the

arrows in Fig 335, DD, DR, RD, RR, *i e* DD, 2DR, RR, which agrees with the experimental result If we represent dominant and recessive factors by A and a respectively, then the expansion of $(A + a)(A+a)$, *i e* $AA + 2Aa + aa$, gives the distribution of pure and hybrid offspring in the second generation

It is worth noting that if the experiment were continued for a number of generations and all the self-fertilised individuals were equally fertile (suppose each produced, say, four offspring) the number of hybrid forms *in comparison with the number of pure forms* would become less and less It can easily be calculated that in the 10th *inbred* generation (11th filial generation) the ratio would be pure dominants hybrids pure recessives = 1023 · 2 . 1023 In the nth inbred generation the ratio would be $2^n - 1 . 2 \quad 2^n - 1$

Mendel's theory can be verified by crossing hybrids with pure dominants If there are produced by the hybrids equal numbers of germ-cells containing the factors D and R, while in the pure dominants all the germ-cells have the factor D, then the chances of dominant germ-cells meeting with dominant or with recessive germ-cells are equal, and the result should be equal numbers of pure and impure dominants in the offspring This is found to be the case Similarly, on crossing hybrids with pure recessives there are impure dominants and pure recessives in equal numbers

The chief results of Mendel's work may be stated thus

(*a*) The idea or conception of pairs of alternative unit characters represented by factors in the germ-cells

They are called unit characters because they (or, rather, the factors representing them) are inherited as units, *i e* they are either inherited or not inherited, they cannot be partly inherited.

(*b*) The idea of dominant and recessive characters. D × R gives D(R) This has sometimes been called the Law of Dominance, but, strictly speaking, there is no such law. Many cases are now known where the hybrid offspring has a character more or less intermediate between the two differentiating characters of the parents (for explanation see § 20) In this case the two pure forms and the ratio 1 2 1 are distinctly recognisable in the second generation F_2.

(*c*) The separation or splitting off of pure forms from hybrids in the second and succeeding generations.

(*d*) The segregation of factors in the germ-cells This is the essential part of what is called Mendel's Law

§ 18. **Allelomorphs, etc.**—The pairs of differentiating characters are now called *allelomorphs*, of which one in each pair may be dominant, the other recessive If the dominant and recessive factors in the germ-cells are represented by A and *a* (or B and *b*, C and *c*, etc) respectively, then the germ-plasm of the zygote and body-cells of a pure dominant will contain the two factors AA, that of a pure recessive *aa*, that of a hybrid A*a* It is only in the germ-plasm of the zygote and body-cells of the hybrid that the two factors A and *a* are associated The meaning of the term zygote is extended from the cell resulting from fertilisation to include the organism developed from it Pure dominants and recessives, therefore, are called **homozygotes** (represented by AA and *aa*), while a hybrid is called a **heterozygote** (represented by A*a*)

The pure dominant is said to be *homozygous* for the character represented by A, the pure recessive homozygous for the character represented by *a* Each germ-cell of a pure dominant receives a single factor A; of a pure recessive a single factor *a*, but in a hybrid the factors A and *a* are separated and pass into different germ-cells This is in agreement with the cytologically observed fact of the reduction of the chromosomes in the formation (in the higher plants) of the spores from which the ♂ and ♀ cells are derived It has to be carefully observed that *germ-cells are always pure*—they never contain both factors of a pair

§ 19. **Di-hybrid Crosses.**—Mendel also carried out an experiment with two pairs of differentiating characters. He crossed a variety of Pea with *yellow* cotyledons and *round* seeds (both dominant characters) and one with *green* cotyledons and *wrinkled* seeds (both recessive characters) He found that with regard to inheritance these pairs of characters were independent of each other. The seeds obtained were all yellow and round, and, therefore, *since these characters depend on the characters of the*

hybrid embryos in the seeds, we may say that the hybrids showed both dominant characters. The seeds obtained from the self-fertilised hybrid plants belonged to four types: (*a*) yellow and round, (*b*) yellow and wrinkled, (*c*) round and green, (*d*) wrinkled and green, in the ratio, approximately, 9 : 3 : 3 : 1—the actual numbers were 315 : 101 : 108 : 32. The groups, however, are not homogeneous, as Mendel showed by continuing the experiment to the next generation. The results arrived at are best displayed by a theoretical explanation; theory and experiment are in close accord.

If we represent the two pure forms crossed by AABB and *aabb* (A yellow, B round, *a* green, *b* wrinkled—or we might use the letters Y, R, *g*, *w*), the offspring forming the first or hybrid generation F_1 will be represented by A*a*B*b* (Y*g*R*w*) and show both dominant characters. The hybrid germ-cells on segregation will be in equal numbers of the four types AB, A*b*, *a*B, *ab* (these are all the possible combinations of the factors—A*a* and B*b* will not occur). In fertilisation any one of four male cells of these types will fuse with any one of four corresponding female cells, and hence there will be 16 possible combinations, some, however, being identical. These combinations are quite easily worked out; they are also given by expanding $(AA + 2Aa + aa) \times (BB + 2Bb + bb)$. They are:—

(1) 1 AA BB—homozygous for both A and B (pure type) (2) 2 AA B*b*—homozygous for A only (3) 2 A*a* BB—homozygous for B only (4) 4 A*a* B*b*—heterozygous for both characters	these 9 forms have both A and B—hence all yellow and round
(5) 1 AA *bb*—homozygous for both A and *b* (pure type) (6) 2 A*a bb*—homozygous for *b* only	these 3 have A and *bb*—hence all yellow and wrinkled.
(7) 1 *aa*BB—homozygous for both *a* and B (pure type) (8) 2 *aa* B*b*—homozygous for *a* only	these 3 have B and *aa*—hence all round and green.
(9) 1 *aa bb*—homozygous for both *a* and *b* (pure type)	1 wrinkled and green.

The table clearly shows what types are included in the groups forming the 9 3 3 : 1 ratio of the second generation The following points should be carefully noted — (1) How complicated is the experimental work in connection with even two pairs of characters · (2) only four in 16 offspring are homozygous or pure for two characters, the others are heterozygous with respect to, at least, one pair of characters, and there will therefore be further segregation in succeeding generations (3) in addition to the two pure parental types, two other pure types AA*bb* and *aa*BB, representing new combinations of the characters, separate out, it is believed that this indicates one way in which new varieties or species may arise, it is also of great practical importance; for example, by crossing two varieties of wheat, each of which possesses a good quality and a bad quality, it is possible by recombination to produce a variety possessing the two good qualities without the bad.

§ 20 **Recent Work.**—Mendel's Law has now been found to hold good in so many cases formerly regarded as obscure or as inexplicable by it that many now regard it as a principle of general application to inheritance in all cases of sexual reproduction, and believe that in conjunction with environmental modification it is sufficient to explain the various " modes of inheritance "

Mendelian theory, however, has been considerably expanded and modified in recent years. It was originally believed that dominant and recessive characters were both represented by definite factors in the germ-plasm, and some still hold this view. There are, however, strong reasons for believing that there is only one factor involved in each pair of differentiating unit characters, and that the dominant and recessive characters are determined by the *presence* and *absence* respectively of the factor This would give a complete explanation of why we never find A and *a* in the same germ-cell In accordance with this view certain terms have been applied to the hybrid and the two pure types The pure dominant with a double dose of the factor (AA) is called *duplex*; the hybrid with

a single dose (Aa) *simplex*, and the pure recessive in which the factor is altogether wanting (aa) *nulliplex*. A single dose of the factor may be sufficient to determine the full expression or development of the dominant character, and in this case the hybrid will, with respect to the character, resemble the pure dominant parent, but, if not, the hybrid offspring will be more or less intermediate

It is now known in certain cases that a character may depend not on a single factor, but on two, three, or more factors Indeed, it has even been maintained recently that most characters depend on a large number of factors and that dependence on one factor is exceptional It will be evident, from what has been said, that the investigation or analysis of such cases presents great difficulty and, if many factors be involved, may be well-nigh impossible

Another phenomenon is that of *linkage* or gametic coupling, in which two characters are always associated owing to the fact apparently that the factors on which they depend are in the same chromosome and appear to be linked together in some way It has been found also that there appear to be certain factors which prevent or tend to prevent the development or expression of certain other factors, and hence are called limiting, inhibiting or *lethal factors* The non-development of fertile pollen in some hybrids, for example, has been ascribed to the presence of a lethal factor

Certain cases of *reversion on crossing* have now been explained on Mendelian principles A character present in an ancestor and depending on the presence of two complementary factors would be lost if, in the course of descent, the factors were separated, but would reappear if the two factors happened on crossing to be brought together again Some cases of reversion, however, are due simply to the expression of a recessive character which has long been latent.

§ 21. **Mendelism and Biometry.**—It has been said that, while formerly it was necessary for Mendelism to reconcile its results with those of Biometry, now it is necessary for Biometry to reconcile its results with those of Mendelism There is general agreement on one point at least. Biometry does not in any way give

a physiological explanation of inheritance such as Mendelism gives—it gives no information on the mechanism of heredity Its main results are generalisations based on statistical data It is often said that while Mendelism endeavours to arrive at a correct knowledge of the germinal constitution of individuals and hence to predict the characters of their offspring, Biometry gives an estimate of the probable character of an individual from a knowledge of his ancestors.

Many are agreed that when a Mendelian result can be obtained it is much to be preferred to a biometrical one, but point out that in cases where characters depend on many factors, rendering a Mendelian analysis practically impossible, a biometrical result would have a distinct value Others would maintain that, inasmuch as Biometry, making no distinction between environmental fluctuations and variations, is not sufficiently critical of its data, and has, moreover, a conception of inheritance at variance with that of Mendelism, it is unscientific and its results are biologically valueless

§ 22 **The Lamarckian Factor in Evolution.**—The modern form of Lamarckism, accepted by some biologists (Neo-Lamarckians) as an important subsidiary factor in Evolution, has already been indicated (§ 6). It is contended that the Lamarckian Factor, if accepted, would provide a much better explanation of certain phenomena and of the evolution of certain classes of characters and structures than either the Darwinian Theory or the Mutation Theory further, that the study of Palaeontology (including Palaeobotany) shows apparently that Evolution has occurred largely, not by the development of anything really new, but by the modification and adaptation of existing structures, and that this is in harmony with the Lamarckian Principle.

§ 23. **The Darwinian Theory (1859**).—Darwin gave some consideration to the "single variations" (now included in Mutations) which sometimes occur, but considered that they were of little importance in evolution as they occurred so seldom and would be immediately swamped by inter-crossing with the parent forms He also accepted to some extent Lamarck's Principle as a subsidiary factor. But he relied mainly on the continuous selection of small individual variations see Chap XVIII) The *Neo-Darwin-*

ians (including Wallace and Weismann) repudiated the Lamarckian Factor altogether and laid down Natural Selection as the all-sufficient factor.

Of course, Natural Selection can only act on variations that appear; variation and heredity are the two conditions of Evolution. But the Neo-Darwinians believed the action of Natural Selection to be cumulative and that the offspring of selected individuals *tended to vary in the same direction*, so that the varying character was gradually strengthened and intensified. There was thus a tendency to magnify the rôle of Natural Selection and to think of it as a *cause* instead of merely as a factor.

Some Darwinians and Neo-Darwinians would now admit that along with the Natural Selection of small continuous variations, mutation plays an important part in the origin of new varieties and species.

The Selection Theory did not meet with universal acceptance. It was criticised from various points:—(1) it was difficult to understand how small individual variations could have selection value or afford a handle to Natural Selection: (2) it was difficult to understand how concomitant selection of small individual variations in different characters could take place and eventually result in structures sharing in a common function; such an acute thinker as Herbert Spencer felt this difficulty keenly and he fell back on the Lamarckian Factor. (3) many structures are met with which have no apparent utility, and it is difficult to see how Natural Selection could have had anything to do with their appearance. (4) there was the difficulty that small individual variations would be liable to be swamped by intercrossing, additional factors such as *isolation* of the varying forms and (by Weismann) *germinal selection* were proposed to get over this difficulty: (5) there were the facts of regression: and, later, (6) Johannsen's demonstration that Natural Selection is ineffective in a pure line, and that there is a definite limit to its action in a population, together with the probable conclusion that continuous variation is largely of the nature of environmental modification. It was the recognition of some of these difficulties that led to the renewed study of

Variation and Heredity towards the close of last century which ultimately resulted in the appearance of the Mutation Theory.

§ 24. **The Mutation Theory** (see § 8) got rid of the difficulties mentioned above. Mendelism greatly helped by demonstrating that there was no danger of a new character, if it were a Mendelian character, being swamped by intercrossing with the parent form. According to this theory Natural Selection is still a factor, but its action is restricted to the elimination of forms, due to mutation, which are not fitted for their environment As de Vries expresses it, "Natural Selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest"

We have seen (§ 19) that new forms or species may arise by new combinations of characters in crossing or hybridisation. By some these new combinations, depending on new grouping of factors in the germ-cells, are included under the term mutations Usually, however, by mutations are meant really new characters appearing more or less suddenly as a result of some previous change in the germ-cells (premutation). In the *Combinations* referred to there is nothing really new, simply a rearrangement of characters Mutationists generally do not regard this as an important source of new species in Nature

The new theory did not explain adaptation as it was somehow felt the Selection Theory did. There was, at first, a tendency amongst mutationists to minimise this difficulty by maintaining that, while organisms show adaptation to environment in a general way, there had been much exaggeration with regard to its finer aspects. But, even allowing for much exaggeration, there is abundant evidence of adaptation everywhere in nature, and it has to be accounted for. Some would fall back frankly on the Lamarckian Factor. Recently the interesting suggestion has been made that new forms simply occupy and multiply in regions or localities for which they happen to be fitted.

It seems probable, however, that the explanation is to be

found in the recognition of the occurrence in nature of numerous small, as well as large, mutations, on which Natural Selection will act. From this point of view the Mutation Theory might be regarded (as it is by many) as a modification and development of Darwin's Theory, in which definite variations or mutations, large and small, take the place of small individual variations, and in which the action of Natural Selection is correspondingly restricted.

§ 25. **Origin and Causes of Mutations.**—It will be evident that if we accept the Mutation Theory it is more than ever necessary to determine the origin and causes of variation or mutation, for it is on mutation that the chief stress is laid Some recent workers believe that they have evidence of the origin of *new factors*, both dominant and recessive, by definite changes, probably chemical in nature, occurring in certain parts of the chromosomes, factors either entirely new or due to modification of existing factors The changes may apparently be induced by internal or external stimuli. There is, at least, some evidence to show that mutations may be induced by external influences It has, however, to be noted that the great bulk of these mutations behave as Mendelian recessives, and, as we have said, there is good reason for believing that a recessive character implies the lack or absence of a factor On this view such mutations would be due to loss of factors (negative or retrogressive mutations—*e.g* hairless varieties, white-flowered varieties, etc.).

With regard to mutations behaving as Mendelian dominants (positive or progressive mutations), many critics maintain that they may arise in various ways, not necessarily by the appearance of new factors, and that there is at present no convincing evidence of the appearance of new factors The Oenothera mutations of de Vries, for example, are by many believed to be due to Mendelian segregation as the result of previous crossing—the original parent forms no longer being in existence. This question of the origin of factors is the fundamental one in the study of variation.

§ 26 **The Crossing or Hybridisation Theory of Evolution.**—It has recently been maintained by Lotsy and others that new species are due solely to crossing and Mendelian segregation At the reducing division and at fertilisation there would be redistribution and mixing of parental factors amply sufficient to provide for the appearance of new forms "Everything apparently new depends on a recombination of factors already present in the parents 'The cause of evolution lies in the interaction of two gametes of different constitution'" According to this view there is *now* no such thing as germinal variability The germinal factors are constant things, *no longer* subject to change or modification but, like the atoms of the chemist, they can be redistributed and built up into new combinations

This, of course does not go to the root of the matter Even if we accept the theory we must still seek for the origin of the germinal factors Did they originate in the primitive unicellular organisms from which plants and animals were evolved, and in which the living protoplasm would be more subject to modifying influences? It is evident that our ignorance of variation is immense Some practically give up the problem by assuming that living protoplasm possesses an inherent variability, or that all variability, as well as all response to environment, is due to some inherent vital impulse

APPENDIX.

I GENERAL ADVICE TO THE STUDENT

§ 1 **Reading**—The necessity of *careful* reading cannot be too strongly insisted on The student should be ever on his guard against the tendency to rapid reading and hasty assimilation Before passing from one part of the subject to another he should make sure *as far as he can* that he has understood what he has read A habit of skipping difficulties is easily acquired and not easily overcome Of course there may be many cases where even the most diligent application will fail to clear up difficult points and where persistence in wrestling with them only results in a waste of time In such cases the student should for future reference make a note of the points he has failed to master It may be that a wider knowledge of the subject will make them clear

Special reference may here be made to the first two chapters of the present text book These chapters deal with general facts and principles and it is not expected that at the first reading the student will acquire a perfect knowledge of their contents They may be used for purposes of reference and should be very carefully revised at a later stage

However careful the reading be it is perfectly useless unless accompanied by diligent practical work This will be specially dealt with in Sections II and III of the Appendix

§ 2 **Sketches and Drawings**—In connection with the practical work the student should besides keeping a record of his experiments and observations make clear, outline pencil drawings of the specimens examined or the sections

cut. The making of sketches gives precision to the work besides helping the memory; it impresses on the student's mind not only the more important points, but also many details which might otherwise be overlooked. It is advisable that the sketches should be drawn, wherever possible, to some definite scale.

§ 3 **Test Questions.**—Merely verbal knowledge should be avoided, *i.e.* knowledge which can be reproduced by the student only in words and sentences more or less nearly resembling those which he has read. He should be able to express his knowledge in words of his own. This faculty is one test of real knowledge, and will prove invaluable when the student has to deal with *general* questions—that is to say, questions which are framed with a view to testing general knowledge, and which are not as a rule specially dealt with in text-books.

Such, for example, are questions dealing with the comparison of certain types or structures To answer these satisfactorily the student must be able to set down alongside of each other all the important resemblances or differences exhibited. It is in such general questions, as a rule, that the student who is a mere echo of a text-book comes to grief.

The moral of all this is that the student should be constantly testing his knowledge by trying to write down what he knows on various parts of the subject Wherever it is possible he should make a point of illustrating his work by outline drawings.

§ 4. **Botanical Terms—Greek and Latin Roots.**—Many botanical terms have departed so far from their original meanings, as implied in their etymology, that the student must get to know them in the same way as he would get to know the words in learning a new language. Frequently, however, a knowledge of the derivation of botanical terms is really helpful; for this reason we give here a table of Greek and Latin roots which may be of service to the student.—

GREEK

a-, *without* (apetalous), **acro-**, *summit* (acropetal), **actino**, *rayed* (actinomorphic), **adelphos**, *brother* (monadelphous), **amphi**, *both* (amphibious), **ana**, *up* (anabolism), **andr**, *of man* or *male* (andrœcium), **anemos**, *wind* (anemophily), **angios** *a vessel* (angiosperm), **anti-**, *opposite* (antipetalous), **apo**, *away from* (apocarpous) **bio**, *life* (biology), **blema**, *covering* (epiblema), **bolos**, *a throwing*, **carp**, *fruit* (epicarp), **cata**, *down* (catabolism), **chlamys**, *a cloak* (archichlamydeæ), **chloro-**, *green* (chlorophyll), **chromo**, *colour* (chromoplast), **cleisto**, *closed* (cleistogamous), **cyto**, *cell* (cytoplasm), **derma**, *skin* (epidermis), **di**, *twice* (dicotyledon), **dich**, *apart* (dichotomous), **dynamis**, *strength* (tetradynamous), **endo**, *within* (endocarp), **epi**, *on* (epidermis) **ergon**, *work* (energy), **gamos**, *marriage* (polygamy), **ge**, *earth* (geotropism) **gen**, *producing* (endogenous, oxygen), **gyn**, *of woman* or *female* (gynæceum) **helios** *sun* (heliotropism), **heteros**, *different* (heterogamous) **histos**, *web tissue* (histology), **homos**, *same* (homology) **hypo**, *under* (hypodermis), **logos**, *science* (physiology), **mega**, *large* megaspore) **meros**, *part* (mericarp), **meso**, *middle* (mesocarp) **micro**, *little* (microspore), **mono**, *single* (monadelphous **morphe**, *form* (morphology), **oecium** (**oikos**), *house* (andrœcium) **oid**, *like* (bacteroid) **oon**, *an egg* **orthos**, *straight* (orthostichies) **peri**, *around* (pericycle) **phile**, *loving* (hydrophilous) **phobe**, *hating* (photophobic), **phore**, *carrying* (carpophore) **phyll** *leaf* (mesophyll) **phyte**, *plant* (spermaphyta) **plasma** *anything formed* (protoplasm) **pod**, *foot* (monopodial) **poly**, *many* (polypetalous), **protos**, *first* (protoplasm) **pseudo**, *false* (pseudocarp) **rhiza**, *a root* (rhizoid) **sapros**, *putrid* (saprophyte) **schizo**, *split* (schizocarp), **scleros** *hard* (sclerenchyma), **sperma** *seed* (endosperm) **stichos**, *a row* (orthostichies) **syn**, *together with* (syncarpous) **tetra**, *four* (tetradynamous) **thec**, *a case* (theca) **tropos**, *direction* (heliotropism), **xero**, *dry* (xerophilous), **zygon**, *a yoke* (zygomorphic), **xylon**, *wood* (xylem)

LATIN

ad, *to* (adhesion) **albus**, *white* (alburnum), **amplexus**, *embraced* (amplexicaul) **arena**, *sand* (arenaceous), **argilla**, *clay* (argillaceous) **auriculus**, *little ear* (auriculate); **axilla**, *armpit* (axil, axillary) **bacillum**, *little staff* (bacillus), **bi**, *twice* (bifid, bipinnate), **bulbus**, *onion* (bulb), **caducus**, *fallen* (caducous) **capillus**, *hair* (capillary), **capitulum**, *little head* **capsula**, *little box* (capsule), **carcer**, *prison* (carcerulus), **carn**, *flesh* (carnivorous), **caruncula** *small piece of flesh* (caruncle) **caulis**, *stem* (caulicle) **com** (**cum**, *with* (compound collateral) **corona**, *crown*, **corolla**, *little crown* **corymbus**, *bunch of flowers* (corymb), **cutis**, *skin* (cuticle), **decurro**, *to run down* (decurrent), **decusso**, *to divide crosswise* (decussate), **dehisco**, *to open* (dehiscent), **duramen**,

hardness; **equito,** *to ride on horseback* (equitant); **ex,** *without* (exalbuminous); **-fid,** *cleft* (pinnatifid); **fistula,** *pipe* (fistular); **flaccidus,** *withered* (flaccid); **flos,** *flower* (floral); **folia,** *leaf* (foliage); **folliculus,** *little bag* (follicle); **fugo,** *to flee* (fugaceous); **glaber,** *smooth* (glabrous); **glaucus,** *bluish grey* (glaucous); **hasta,** *spear* (hastate); **haustus,** *drawing up water* (haustorium); **hispidus,** *bristly* (hispid); **humus,** *soil* (humus); **imbrex, -icis,** *a roof tile* (imbricate); **impar,** *unequal* (imparipinnate); **inter,** *between* (intercellular); **involucrum,** *cover* (involucre); **labium,** *lip* (labiate); **lignum,** *wood* (lignified); **ligula,** *strap* (ligulate), **loculus,** *little place* (trilocular); **nectar,** *honey*; **nodus,** *knot* (node); **nuto,** *to nod* (nutation); **nux,** *nut* (nucellus); **ovum,** *egg* (ovule); **papilio,** *butterfly* (papilionaceous); **par,** *equal* (paripinnate); **paries,** *wall* (parietal); **pelta,** *shield* (peltate); **persona,** *mask* (personate); **peto,** *to seek* (acropetal), **pinna,** *wing* (pinnate), **pluma,** *feather* (plumule); **pulvinus,** *cushion*; **pyxis,** *box* (pyxidium); **racemus,** *bunch of grapes* (raceme); **radix,** *root* (radicle); **renes,** *kidney* (reniform), **rota,** *wheel* (rotate); **sagitta,** *arrow* (sagittate); **sectus,** *cut* (pinnatisect); **serra,** *saw* (serrate), **siliqua,** *pod* or *shell*; **subula,** *awl* (subulate); **umbella,** *parasol* (umbel); **urceolus,** *little pitcher* (urceolate); **vas,** *vessel* (vascular), **versatilis,** *revolving* (versatile); **verticillus,** *whirl of a spindle* (verticillate)

§ 5. **Supplementary Reading.**—To such students as may be desirous of further extending their botanical studies the following books are recommended :—

Willis' *Flowering Plants and Ferns* (Cambridge Natural Science Manuals, 20s), Strasburger's *Text-book of Botany* (Macmillan, 31s 6d), Scott's *Introduction to Structural Botany*, Two Parts (Black), Coulter, Barnes and Cowles, *Text-book of Botany*, New York ; and a good local flora

II. Notes on Practical Work.

§ 6. **Examination of Plants.**—The student should devote a considerable amount of time to the study of complete plants, and the examination of special parts. He should carefully notice the different kinds of roots and stems, and accustom himself to the use of the various terms explained in the text. Bulbs, tubers, corms, rhizomes, suckers, etc , should be studied, and their special features

recognised. The morphological value of spines or thorns, tendrils, and other specialised structures, wherever specimens present themselves, should be clearly made out. The form, arrangement, and venation of leaves; branching; the position of buds, stipules, bracts, etc ; the forms, etc., of corolla, androecium, and gynaeceum; the seed and fruit, etc ;—all these should be subjected to careful examination.

In the examination of minute or crowded parts, as, for example, in the case of many flowers, it will be found not only convenient, but necessary, to use a small **hand-lens.** A very convenient folding form, with three glasses, can be obtained from any dealer. For finer work, a simple dissecting stage, with lenses, can now be obtained for a few shillings.

§ 7. **Physiology.**—A practical knowledge of the nutrition and growth of plants is essential. The student, therefore, should carry out as many of the simple experiments described in Chapters VII. and VIII as he can, and devise others for himself These chapters should be studied concurrently with Chapters III - VI

§ 8 **Microscopic Work.**—We cannot give here full detailed directions serving to initiate the beginner in the mysteries of section-cutting, etc An excellent book for practical work is Cavers . *Practical Botany* (Univ. Tutorial Press, 6s 6d)

We shall confine ourselves here to a few notes on fundamental details.

§ 9 **Apparatus.**—The following are necessary .—

(*a*) A good microscope with lenses $\frac{1}{2}$ and $\frac{1}{6}$ inch focal distance

(*b*) Two *good* razors, slightly hollow-ground.

(*c*) Glass slides, $3'' \times 1''$; cover-glasses, $\frac{7}{8}''$ diam. or sq.

(*d*) Small forceps, dissecting needles, and scalpels

(*e*) A few deep watch-glasses; small brushes, a clean piece of soft linen.

(*f*) Pickle jars, methylated spirit, formalin (see § 12).

(*g*) Small bottles (with dipping rods) containing iodine

solution, aniline sulphate (or chloride), Schulze's solution, glycerine, etc.

A really serviceable microscope for all ordinary work is Leitz's Student's Microscope, with eye-pieces 1 and 3, and objectives 3 and 7.

Information with regard to reagents will be found in the practical text-book.

§ 10. **Cutting and Mounting Sections.**—At first the student should content himself with sections simply stained with iodine or aniline sulphate and mounted in glycerine Only if time permits, and after considerable experience in this method, should he attempt more elaborate methods of staining and mounting

In taking a section, the tissue to be cut should be held between the thumb and fingers of the left hand; the razor in the right hand The tips of the four right fingers should rest on the back of the razor, and the thumb in front, just behind the cutting edge. The cutting edge is therefore directed inwards, towards the operator. The arms should be brought close up to the body. Tissue and razor should both be wet with alcohol The blade of the razor may rest gently on the forefinger of the left hand with the edge against the tissue. Then the razor should be drawn through the tissue with a sliding movement. *With practice*, extremely thin sections may be cut.

The sections should be removed from the razor by means of a brush, and placed in a watch-glass containing alcohol or water. Several may then be transferred to a slide and examined in water under the low power, so that the best may be selected. By means of the linen cloth the excess of water may be removed, and iodine or other reagent added according to the special points which the student wishes to determine. The reagent should then be washed off with water, the excess of water removed, a drop of glycerine added, and finally the cover-glass put on.

The section should always be mounted in the centre of the slide. The cover-glass should be rested on its edge and let down gradually by means of a needle The section

must not be allowed to get dry during the process, or air-bubbles will make their appearance. If these do appear, soaking the section for some time in alcohol will remove them. The cover-glass must be perfectly clean, and the upper surface dry.

Neatness and cleanliness are of great importance in practical work. At first the student will find that his sections are rather thick, and often obliquely cut. These are difficulties which can be got over only by care and practice. He should not attempt to draw a bad section.

Very slender or delicate tissues should be cut by embedding in pith or carrot. More elaborate methods may be passed over in early stages of practical work. If carrot be used, a piece $1'' \times \frac{1}{2}'' \times \frac{1}{4}''$ will be found convenient.

§ 11 **Reagents.**—The effects produced on cell-walls and cell-contents by iodine solution, aniline sulphate, Schulze's solution, etc, should be studied. The tests for starch, proteid, cellulose, cork, mineral crystals, are important.

§ 12 **Material.**—Fresh material may and sometimes must be used. In many cases, however, it is better and more convenient to use "pickled" material. The pickling fluid used for ordinary work is ordinary methylated spirit. Stems, roots, leaves, etc, preserved in this way in glass jars are always ready for use. Delicate plants or parts of plants (flowers, etc) may be preserved in four to six per cent solution of formalin (formic aldehyde); formalin as sold is a forty per cent solution. This method has the advantage of preserving colours. Types such as *Vaucheria*, *Spirogyra*, *Œdogonium*, *Eurotium*, Yeast, must be examined in the living state.

The student is advised to obtain material himself, as far as possible. With the Angiosperm, *Pinus*, Fern, and *Agaricus* there is no difficulty. *Marchantia*, *Funaria*, *Œdogonium*, *Spirogyra*, and *Vaucheria* are also easily found. Fern-prothalli can usually be obtained in abundance on the damp walls or on the soil of flower-pots in fern-houses. Directions for obtaining *Pythium*, *Eurotium*,

etc., are given in our descriptions of these types. Yeast may be obtained from a baker.

§ 13. **Practical Work on Angiosperms.**—As the student may be in some doubt as to the practical work which should be undertaken in connection with the Angiosperm, the following list may be of service.

Stems.—Transverse and longitudinal sections of various Dicotyledon stems, herbaceous and woody, and of various Monocotyledon stems. For comparison sections of aquatic stems should also be cut The beginning of secondary growth in Dicotyledons should be studied.

Buds.—Longitudinal sections Try to make out the meristematic regions.

Roots.—Transverse sections of various roots The apical meristem can be studied in *median* longitudinal sections of the radicles in Maize, Almond, Sunflower, and Castor-oil seeds

Leaf:—Sections of petiole and lamina; strip off part of epidermis to see stomata, etc.

Flower.—Sections of ovaries and anthers. The structure of the ovary, the placentation, the form and structure of the ovules, should be recognised. The form and structure of the ovule can usually be readily made out in sections of ovaries, or, if the ovules are small, by examining entire after treatment with dilute potash solution.

Seeds.—In examining a seed the student should determine by means of sections and staining—(*a*) Dicotyledonous or Monocotyledonous, (*b*) albuminous or exalbuminous, (*c*) the nature of the food-material.

Contents of cells and cell-walls.—These should be very carefully studied in connection with the above. To see such bodies as cystoliths and raphides the student should try to obtain the material mentioned in the text-book.

III. Descriptive Botany.

§ 14. **Description of Plants.**—The art of describing plants consists simply in being able to make use of the proper terms in a neat, orderly way. An elaborate description is not expected of the elementary student The following scheme simply indicates the order on which such a description should proceed it is not to be regarded as a form for plant-description, to be rigidly adhered to in all cases.

Root: tap or adventitious? branched or unbranched? the special form—tuberous, fleshy, fibrous, etc.? annual, biennial, or perennial?

Stem: kind of stem—*i e* is it erect, prostrate, or climbing, a rhizome, corm, or bulb, etc? herbaceous or woody? cylindrical, angular, or compressed? hairy or glabrous? branched or unbranched (the branching may be described)? If herbaceous, is it solid, hollow (fistular), or jointed? If climbing, how does it climb? Does it bear cladodes, tubers, spines, etc.?

Leaf: deciduous or evergreen? radical, cauline, or ramal? alternate, opposite (superposed or decussate), or verticillate? petiolate or sessile? stipulate or exstipulate (the stipules may be described)? sheathing, connate, perfoliate, ligulate, etc.? simple or compound?

If simple, outline of lamina (*i e.* linear, oval, etc, or pinnatifid, palmatifid, etc.—if incised, the outline of the lobes, partitions, or segments may be indicated)? venation? margin? apex? surface (glaucous, hairy, etc)?

If compound, pinnate or palmate? paripinnate or imparipinnate? number and arrangement of leaflets? *Leaflets*—sessile or stalked? outline? venation? margin? apex? surface?

Inflorescence: definite, indefinite, or mixed? kind of inflorescence?

Flowers: sessile or pedicellate? bracteate or ebracteate (if bracteate, the bracts may be described)? complete or incomplete? hermaphrodite or unisexual? actinomorphic, zygomorphic, or asymmetrical? cyclic hemicyclic, or spiral? heterostylic? any other general character?

If there are two kinds of flowers, after giving common characters as above, describe separately.

Calyx: poly- or gamo-sepalous? green or petaloid? if polysepalous, the number, outline, and apex of the sepals? if gamosepalous, the special form or nature of the incision? inferior or superior? æstivation?

Corolla: regular or irregular? if irregular, zygomorphic or asymmetrical? poly- or gamo-petalous? if polypetalous, number and outline of petals, or any special terms? if gamopetalous, special form or incision? corona or other special features? hypogynous, perigynous, or epigynous? æstivation?

Perianth: described similarly, except that the terms poly- or gamo-phyllous must be used.

Andrœcium: number of stamens? or indefinite? polyandrous, syngenesious, or adelphous? epipetalous, epiphyllous, hypo-, peri-, or epi-gynous? special characters? filament? fixation of anther? dehiscence?

Gynæceum: mono- or poly-carpellary? if the latter, apo- or syn-carpous? *Ovary*—unilocular or multilocular? superior or inferior? *Ovules*—number? or indefinite? form? *Placentation? Style? Stigma?*

Seed: albuminous or exalbuminous?

Fruit: kind of fruit?

Nectaries may be described in connection with corolla stamens, or pistil, as seems convenient. The probable mode of pollination, and of the dispersal of the seed or fruit, should be mentioned, along with a description of any special mechanical contrivances in connection with these processes.

§ 15. **Examples.**—The following descriptions of well-known plants will serve as examples.—

(1) **Root**: a fibrous branched tap-root, perennial
Stem: erect; branched; angular; herbaceous above, woody below; slightly hairy; perennial.
Leaves: herbaceous; cauline; shortly petiolate; exstipulate; simple; lanceolate; unicostate; reticulate; acute; entire; slightly hairy.
Inflorescence: indefinite—terminal and lateral, more or less corymbose racemes.
Flowers: pedicellate; ebracteate, isobilateral; hermaphrodite.
Calyx: polysepalous; four lanceolate, petaloid sepals in two series, the two inner (lateral) sepals slightly pouched (saccate); inferior.
Corolla: regular, polypetalous, cruciform, consisting of four unguiculate petals; *limb* obovate; hypogynous; imbricate.
Androecium: six stamens in two series, tetradynamous; two short lateral stamens; two pairs, anterior and posterior, of long stamens; hypogynous; *anthers* innate, introrse, with longitudinal dehiscence *Nectaries*, having the form of green, rounded discs, are present at the base of the lateral stamens.
Gynæceum: bicarpellary, syncarpous; *ovary* bilocular, owing to a false septum developed between the placentas, superior; *ovules* ∝, campylotropous, on two parietal placentas; *style* short; *stigma* two-lobed.
Seed: exalbuminous. **Fruit**. an elongated, linear, slightly flattened siliqua.

(2)* **Roots**. adventitious, fibrous, and stout, yellowish
Stem: woody, perennial, underground, covered with brown scales, and throwing out long slender runners which root at the nodes.
Leaves: radical, with long hairy petioles and membranous, lanceolate, petiolar stipules; compound, ternate; *leaflets* nearly sessile, roundish oblong, with unicostate reticulate venation and serrate margin
Inflorescence: panicled, more or less corymbose, cymes borne on erect slender scapes.
Flowers: pedicellate, with membranous bifid bracts; actinomorphic; complete; hermaphrodite; protogynous.
Calyx: gamosepalous, with five membranous, triangular, acuminate segments, green, persistent, inferior; an epicalyx is present consisting of five oblong segments alternating with those of the calyx proper.

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* Adapted from Lindley's *Descriptive Botany*

Corolla: regular, polypetalous, rosaceous, consisting of five white roundish petals inserted perigynously.

Andrœcium: polyandrous, *stamens* ∞, persistent, perigynous, *filaments* short and stiff; *anthers* oval, more or less cordate, dehiscing at the edges.

Gynæceum: polycarpellary, apocarpous; *carpels* indefinite, and borne on a protuberance of the thalamus, with filiform styles and simple stigmas; *ovules* solitary, ascending.

Seed: exalbuminous, dicotyledonous. **Fruit**: a pseudocarp consisting of an etærio of achenes borne on a succulent thalamus.

INDEX OF VERNACULAR NAMES.

[In the following Index the Hindustání names have, on the whole, been given preference to those in the other languages of India. Some plants are included here which are not mentioned in the text. For the page references the student should consult the General Index.]

GENERAL INDEX.

(*Generic names are given in italics, vernacular names in heavy type.*)

INDEX TO SUPPLEMENT.

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